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Regulation of Kentucky bluegrass (*Poa pratensis* L.) morphogenesis by growth retardants and exogenous ethylene

by

Kenneth Lynn Diesburg

A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of

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1987

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GENERAL INTRODUCTION

Research with chemicals that slow the growth of turfgrasses and thereby reduce mowing requirements has been conducted since the mid 1940s. Early materials were growth retardants which stopped or retarded growth by injuring the plants. The net effect was a discoloration of the leaves and reduced recuperative potential. More recent chemicals are closer in being true growth regulators that shift the partitioning of assimilates away from the leaves in favor of roots, rhizomes, stolons or tillers. They result in more dense turf with shorter leaves.

A problem with turfgrass growth retardants has been inconsistent activity, where the effects of a compound vary from no growth inhibition to severe turf injury. This could be due to variations in plant growth phase, climate, or application technique. The growth phase or climate in which turfgrasses are most receptive to regulation has not been fully addressed or identified.

The first hypothesis of this dissertation is that plant growth phase and seasonal climate together influence the response of Kentucky bluegrass (Poa pratensis L.) to turf growth regulators. Kentucky bluegrass was chosen because it is the predominant cool-season turfgrass in Iowa. It has four advantages that make it an ideal research tool. First, the growth of its leaves and stems is primarily one-dimensional, which simplifies the quantification of growth response. Coleoptile growth has been used traditionally for this purpose. Second, the partitioning of assimilates between the leaves and stems of a mature plant can be investigated, something that is impossible to address in

coleoptile growth. Third, the structure of the plant allows exclusive treatment of its only exposed parts, the maturing leaves. The stem apex and crown are shielded by superposing leaves. Fourth, Poa pratensis can be cloned easily, thus eliminating genetic variance in replicated studies. In testing the hypothesis, the objective was to determine the field response of a Kentucky bluegrass cultivar and mixture of cultivars to five turfgrass growth retardants across three growth phases; spring reproductive, summer vegetative, and fall reproduction-inductive.

Of the five materials used, ethephon (2-chloroethylphosphonic acid) is one that expresses true growth-regulating activity. Leaf growth is not stopped. Instead, short undamaged leaves develop while normally inactive internodes elongate.

Ethephon activity is assumed to be derived from its release of ethylene during decomposition in plant tissues. Poovaiah and Leopold (4) showed that treatment of Kentucky bluegrass with ethylene at 5000 μL/L and ethephon at 10,000 mg/L caused qualitatively similar responses. An attempt to verify their results revealed that ethephon effects were always evident while ethylene effects were sometimes absent. Ethephon apparently has a property that promotes greater plant sensitivity to ethylene. This may be due to its slow, continual release of ethylene over a number of days (1, 2, 3), proximity to cell membrane reaction sites, or predisposition of plant tissues to ethylene sensitivity. The assumption of ethylene as the sole stimulus in ethephon effects may not be correct. A definition of the conditions necessary for ethylene sensitivity in Kentucky bluegrass is needed.

The second hypothesis presented in this dissertation is that there are some conditions that will predispose Kentucky bluegrass to greater ethylene sensitivity. The objective was first to identify conditions under which a response to ethylene could and could not be observed and subsequently to test the synergistic effect of ethephon and ethylene applied sequentially. If there is something in ethephon that predisposes Kentucky bluegrass to ethylene sensitivity, then ethylene should cause a more than additive response from a plant previously treated with ethephon.

The two hypotheses and a description of the gas-meting and roomette system constructed to supply continuous flow of precise ethylene levels are each covered by a separate paper in journal form.

PAPER I. SEASONAL APPLICATION OF ETHEPHON, FLURPRIMIDOL, MEFLUIDIDE, PACLOBUTRAZOL, AND AMIDOCHLOR AS THEY AFFECT KENTUCKY BLUEGRASS (*POA PRATENSIS* L.) SHOOT MORPHOGENESIS

Seasonal application of ethephon, flurprimidol, mefluidide, paclobutrazol, and amidochlor as they affect Kentucky bluegrass (*Poa pratensis* L.) shoot morphogenesis[1]

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[1]Contribution from the Department of Horticulture, Iowa State University. Published as Journal Paper No. J- of the Iowa Agriculture and Home Economics Experiment Station, Ames, IA. Project 2232.

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ABSTRACT

A three-year field study was conducted to compare effects of the growth retardants after three application dates representing spring reproductive, summer vegetative, and fall reproduction-inductive growth phases. Amidochlor and mefluidide were most effective in spring, flurprimidol in summer, while ethephon and paclobutrazol had similar effectiveness across seasons. Seasonal changes in growth phase sensitivity of plants to growth retardants is seen as the reason for inconsistent results with general use.

Amidochlor and mefluidide were fast-acting with nearly complete growth restriction during the first two to three weeks after spring application. Mefluidide was also very effective in summer and fall while amidochlor was not. Paclobutrazol and flurprimidol were slow-acting with an average of 16% growth reduction which peaked at 5 and 10 weeks after treatment, respectively. Ethephon effects were strong and continuous throughout the ten-week measurement periods, restricting growth an average of 30%. Mefluidide was the only chemical to reduce turf quality severely. It was also the only chemical to completely prevent heading after both spring and fall treatments. Amidochlor reduced heading by 61% after spring application. Ethephon was the only chemical to stimulate tiller internode elongation. Measurement of individual phytomers within shoots from one sampling provided a continuous record of plant response to treatment over a four-week period. Blade growth was found to be affected more strongly than sheath

growth by all growth retardants except paclobutrazol.

Additional index words: growth retardant, growth regulation, turfgrass

INTRODUCTION

Growth regulators have the potential to save time and money by decreasing mowing frequency. This has positive effects upon many other aspects of turf management: control of growth during wet seasons or periods of rapid growth which are often the most demanding work periods of the year; control of growth on large areas which need not display a manicured surface at all times; suppression of growth in areas that are difficult or dangerous to mow; decrease in labor costs; prolongation of fungicide effectiveness by reducing new growth; increase in abrasion resistance by developing thicker cell walls and more dense plant structures; reduction of stress-related damage to fine turf by increasing resistance to water, salt and other stresses; darker green color; improved chances of a "better lie" by providing sturdier growth and better support of the golf ball (72); reduction in the hazard of operating mowers along highways; and conservation of soil moisture during periods of drought (13). The use of turfgrass growth retardants from the 1950s to early 1970s was restricted to areas of low use and visibility because of phytotoxicity (18, 19, 20, 21, 28, 33, 37, 56, 66, 68, 69, 72, 75). Retardants released in the late 1970s and early 1980s cause less discoloration and thinning of turf, but their activity has been inconsistent (7, 10, 11, 13, 21, 29, 31, 39, 47, 56, 69, 71, 75). Plant receptivity to regulation has been shown to vary among and within species (2, 5, 11, 12, 13, 18, 19, 20, 21, 23, 25, 28, 30, 32, 39, 43, 44, 47, 63, 64, 66, 68, 70, 71, 72, 75). It also may vary with seasonal

plant growth phase or even daily fluctuations in climate. These two possibilities have not been fully addressed. Jagshitz (31) noted that spring treatment with growth regulators had greater efficacy than fall treatment, though no statistical comparisons were made. Schott et al. (57) found no difference in the effects of a light mefluidide rate (0.24 kg/ha) among spring, summer, and fall treatments in a one-year test. Further investigation of these phenomena is warranted. In this study, five growth regulators were tested during three growth phases of Kentucky bluegrass; spring reproductive, summer vegetative, and fall reproduction-inductive (48). The objective was to investigate the effect of application timing and to compare the major effects of each chemical on growth, quality, and plant leaf morphogenesis.

MATERIALS AND METHODS

A field study was conducted at three locations with 'Baron' (1983, 1984) and a blend of 25% by weight each of 'Adelphi', 'Glade', 'Parade', and 'Rugby' (1985) Kentucky bluegrass grown on a Nicollet (fine, loamy, mixed, mesic Aquic Hapludoll) soil with 6.9 pH, 12 mg/kg P, 96 mg/kg K and 23 g/kg organic matter. The test area received 200 kg N/ha yr applied as sulfur-coated urea. The site was irrigated as needed to prevent stress and maintained at a 5-cm mowing height until 7 days after treatment. Data were collected from unmown plots thereafter.

A split-split-plot design with three replications was used with years as whole plots, application dates as subplots, and chemical treatments as sub-subplots. Application dates related to three growth phases; spring reproductive (May, first week), summer vegetative (June, first week), and fall reproduction-inductive (September, last week). Treatments were applied at rates recommended for cool season grasses: ethephon (2-chloroethyl)phosphonic acid at 4.48 kg ai/ha, flurprimidol 50WP α-(1-methylethyl)-α-[4-(trifluoromethoxy)phenyl]-5-pyrimidine methanol at 1.12 kg ai/ha, mefluidide 2S N-2,4-dimethyl-5-{[(trifluoromethyl) sulfonyl]phenyl} acetamide at 0.42 kg ai/ha, paclobutrazol 50WP (2R,3R+2S,3S)-1-(4-chlorophenyl)-4,4-dimethyl-2-(1,2,4-triazol-1-yl)pentan-3-ol at 0.42 kg ai/ha, amidochlor N-[(acetylamino)methyl]-2-chloro-N-(2,6-diethylphenyl)acetamide at 2.80 kg ai/ha, and a distilled water control. They were applied with a pressurized CO_2 sprayer at 2.07 x 10^5 Pa to 1.52 m^2 plots in 1420 L/ha

distilled water solutions through a hand-held boom passing 0.6 m above the ground. Amidochlor was watered into the soil immediately afterward.

Turf quality ratings and canopy heights were recorded 17, 32, and 47 days after each set of treatments, and additionally 72 and 110 days after spring treatments. Spring recovery ratings were made after the previous fall treatments. Data recorded 17, 32 and 47 days after treatment were combined for analysis and reporting of main effects and interactions. Ratings were assigned on a scale of 1 to 9, 1=worst, 5=acceptable, and 9=best using a combination of color, uniformity and density. Canopy height was an average of three random measurements per plot from the thatch surface. Percent heading was estimated during the second week of June from plots treated in spring and the previous fall. Blade, sheath, and internode lengths were measured during the fourth and sixth weeks after each application date. Three shoots per plot were sampled at random and measurements from them were averaged. Blades were measured from the leaf collar to tip and sheaths from the attached node to leaf collar. Root weights were compared twice in the summer 1985 plots from samples taken 17 and 51 days after treatment. Five 2 x 20 cm soil cores were taken randomly within each plot and combined. After rinsing the soil away through 7 mesh/cm screens, root organic matter production was estimated based on the difference between oven dry and ash weights.

RESULTS

Canopy Height and Toxicity

Canopy heights averaged over all seasons, treatments, and dates of measurement were 14% shorter in 1983 and 1984 than those in 1985, while mean turf quality ratings were similar. The retardants, as a group compared to the control, averaged over years and dates of measurement, restricted canopy growth 28% in spring and 21% in summer and fall. Turf quality ratings were reduced 11% in spring and summer and 21% in fall. These seasonal differences were consistent across years (Table 1).

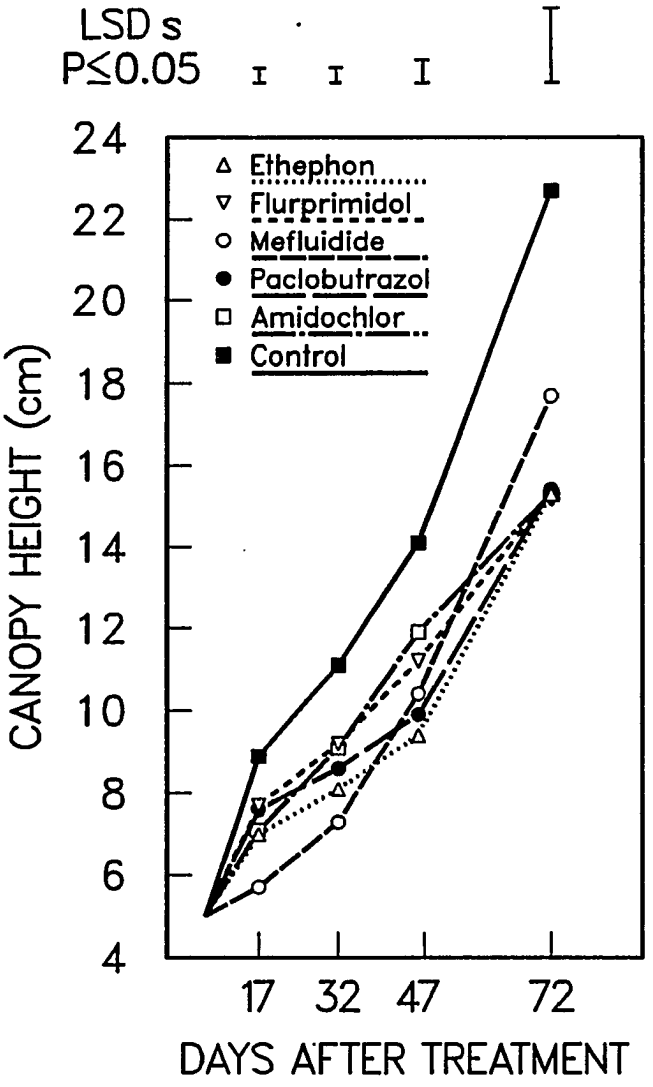
All chemicals reduced canopy heights compared to the control over all three dates of application for at least 72 days after treatment. During the first 47 days, mefluidide or ethephon were the most effective at 32 and 28% less than the control, respectively, followed by paclobutrazol at 24%. Flurprimidol and amidochlor were least effective at 16% less than the control. The materials tested can be divided into three types of growth regulators; fast-, slow-, and continuous-acting (Fig. 1). Mefluidide and amidochlor were fast-acting in that their effects became apparent within 10 and 20 days of treatment and diminished after 32 and 47 days, respectively. Mefluidide had a stronger effect than amidochlor. Paclobutrazol and flurprimidol were slow-acting in that they had little effect on canopy growth the first 17 days. By 32 days, paclobutrazol was becoming more effective whereas flurprimidol took 72 days to reach maximum effectiveness. The strong

Table 1. Analyses of variance of Kentucky bluegrass responses to seasonal growth retardant treatments

Source	df	Mean Squares								
									Spring Recovery	
		Height	Quality	Blade Length	Sheath Length	Intern Length	Heading (Spring Trtmt)	Heading (Fall Trtmt)	Canopy Height 18Apr-28May	Turf Quality 18Apr
Years (Y)	2	31.0*	1.0	8.6*	0.1	0.1	4.3	11.7	6.5	4.7
Error a	6	3.1	0.3	0.9	0.1	<0.1	1.6	3.6	3.3	2.2
Seasons (S)	2	156.0**	20.9**	25.0**	1.4**	<0.1				
Spring vs Summ	1	12.2**	0.5	0.2	2.5**	<0.1				
Spring vs Fall	1	175.5**	27.3**	15.7**	0.3	0.1				
S x Y	4	5.2	0.2	3.4*	<0.1	<0.1				
Error b	12	3.6	0.2	0.7	<0.1	<0.1				
Treatments (T)	5	43.3**	35.7**	37.0**	5.4**	13.4**	90.8**	70.4**	22.4**	5.2**
Control vs Others	1	162.1**	35.0**	128.2**	4.5**	3.0**	38.5**	49.8**	42.2**	2.3
Eth vs Pac[a]	1	3.6*	0.3	26.3**	4.1**	40.7**	0.9	4.9*	29.4**	9.4**
Flur vs Pac	1	6.2**	<0.1	<0.1	<0.1	<0.1	1.4	4.9*	0.3	1.4
Flur vs Control	1	54.0**	5.8**	45.8**	1.5*	<0.1	1.4	4.5*	17.3**	5.6**
Mef vs Amid	1	34.2**	68.2**	20.2**	0.6	<0.1	6.7*	60.5**	1.0	0.9
T x Y	10	2.6**	1.6**	0.7	0.2	0.1**	2.3	6.7**	3.5**	5.8**
T x S	10	7.0**	1.5**	3.2**	0.3**	<0.1				
T x Y x S	20	2.5**	0.7**	0.7	0.1	<0.1				
Error c (b')[b]	90 (30)[b]	0.7	0.1	0.5	0.1	<0.1	1.4	0.7	0.8	0.7

[a]Eth=Ethephon, Pac=Paclobutrazol, Flur=Flurprimidol, Mef=Mefluidide, and Amid=Amidochlor.
[b]Error b' and 30 degrees of freedom for split plot design regarding Heading and Spring Recovery.
*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Figure 1. Turf canopy growth responses to retardant treatments averaged over seasons and years

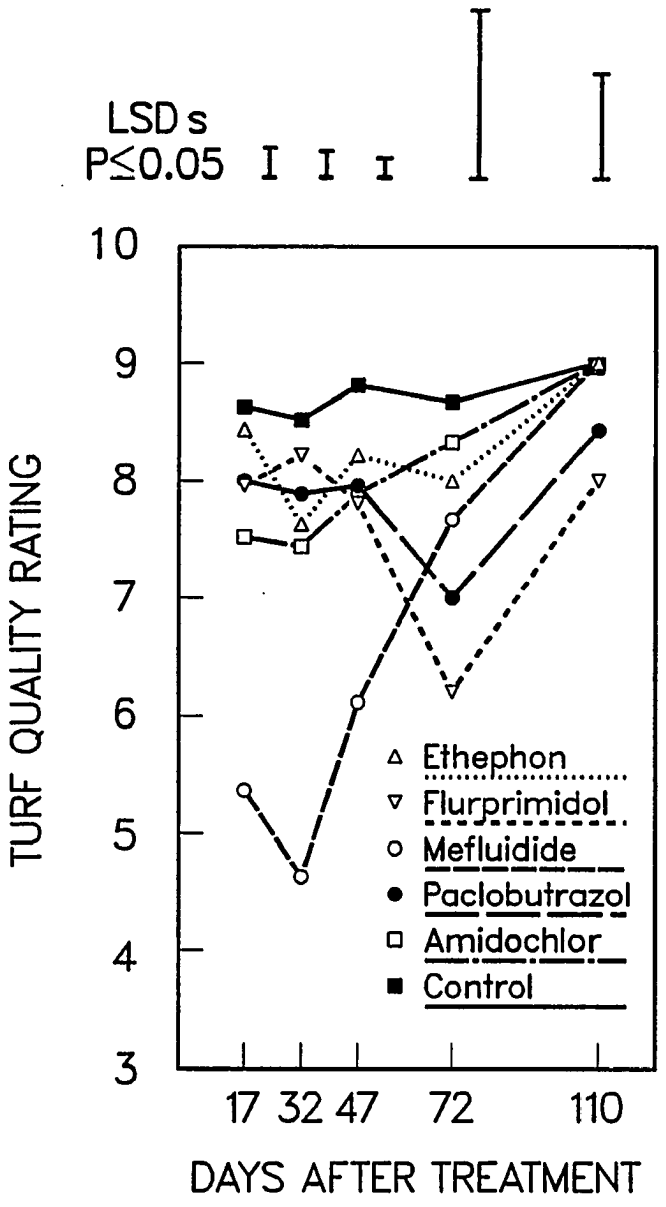

LSD s
P≤0.05
24
22
20
18
16
14
12
10
8
6
4
CANOPY HEIGHT (cm)
Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control
17
32
47
72
DAYS AFTER TREATMENT

effects of ethephon lasted from 17 days after treatment throughout the measurement period. At 72 days canopy heights were similar among all treatments. Plants were recovering from the effects of the fast-acting chemicals, while the slow-acting chemicals and ethephon were still active.

Turf quality over all treatments was positively correlated with canopy height at R=0.64. When a chemical was most active in restricting growth, it was usually causing lower turf quality ratings (Figs. 1 and 2). Ethephon was exceptional in that it was slightly toxic (ratings from 7.6 to 8.2) only during the early part of its activity 32 to 47 days after treatment. From 47 to 110 days after treatment it was the most effective growth inhibitor while not lowering turf quality. Mefluidide was the only chemical to be seriously phytotoxic. Leaves and apical meristems were severely damaged causing the turf to turn brown for a month after treatment.

Most of the studies done with mefluidide (3, 10, 13, 21, 31, 56, 57, 66, 69) have shown similar, short term, strong growth restriction with objectionable lowering of turf quality. Some variations have occurred, however. Christians (10) and Elkins et al. (21) obtained weak restriction of Kentucky bluegrass by mefluidide in one year and strong restriction in another. Experiments in the study of amidochlor (3, 15, 16, 17, 34) agree on the longevity of its effects but disagree on its toxicity. DiPaola et al. (16) found it to be equally toxic as mefluidide, Doyle and Shearman (17) found no toxicity in either chemical, while Bhowmik (3) saw greater toxicity with mefluidide.

Figure 2. Changes in turf quality with time in response to growth retardant treatments, averaged over seasons and years


LSD s
P≤0.05
10
9
8
7
6
5
4
3
TURF QUALITY RATING
Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control
17 32 47 72 110
DAYS AFTER TREATMENT

Diesburg and Christians (15) applied amidochlor at four times the recommended rate for Kentucky bluegrass on six different springtime dates spaced three days apart and found the same low toxicity as with the normal rate. Several publications (10, 13, 30, 61, 70, 71) record similarly long term flurprimidol and paclobutrazol effects although the degree of growth inhibition varied. Toxicity of these chemicals was usually low, but Symington (60, 61) found them to be more phytotoxic than mefluidide. The unique continuous effects of ethephon have been reported by many researchers (10, 13, 15, 29, 32, 37, 49, 63, 64, 71, 72). They agree in its lack of toxicity but disagree in its effectiveness in restricting canopy growth.

Seasonal restriction of canopy growth varied among the chemicals (Fig. 3). Amidochlor was especially effective in the spring while mefluidide excelled in spring and fall. Flurprimidol was most effective in summer. Data not presented showed that mefluidide effects diminished quickly in summer between 17 and 32 days after treatment, and flurprimidol effectiveness in summer was seen 32 to 47 days after treatment. The effectiveness of either ethephon or paclobutrazol was similar across seasons.

All chemicals were more phytotoxic in fall than in spring or summer, with the exception of amidochlor which was equally toxic in spring and fall (Fig. 4). Mefluidide caused severe injury in all seasons. The other chemicals behaved as a group with turf quality ratings similar to the control in spring while 6% and 14% less than the control in summer and fall, respectively.

Figure 3. Mean seasonal turf canopy heights in a 47 day period after growth retardant treatments, averaged over years. The LSD is among treatments within a season

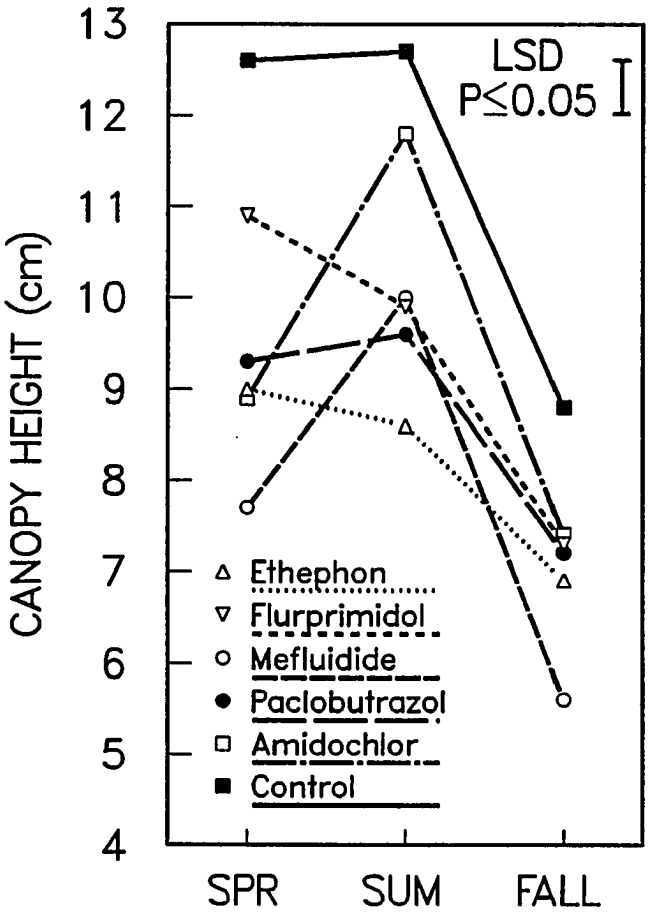
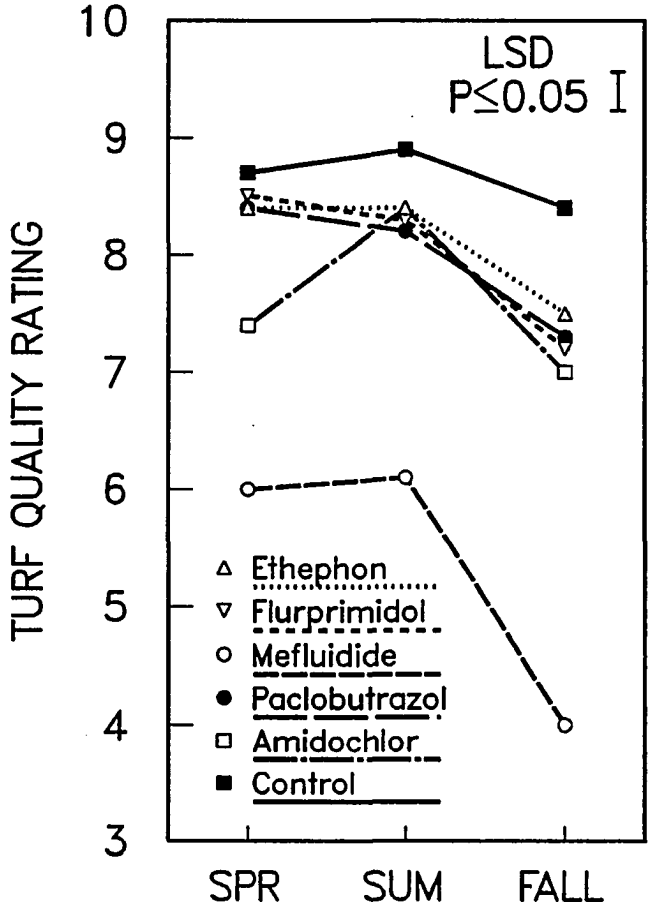

CANOPY HEIGHT (cm)
13
12
11
10
9
8
7
6
5
4
LSD
P≤0.05
Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control
SPR
SUM
FALL

Figure 4. Mean seasonal turf quality ratings in a 47 day period after growth retardant treatments, averaged over years. The LSD is among treatments within a season


10
9
8
7
6
5
4
3
TURF QUALITY RATING
LSD
P≤0.05
Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control
SPR
SUM
FALL

Seasonal effects of all growth regulators on canopy height and turf quality was consistent among years as shown by the lack of season-by-year interactions (Table 1). There were times with each chemical, however, when seasonal activity was either slightly stronger or more rapid in one year than in another. Ethephon activity in restricting canopy growth was weak in fall 1985, as was that of mefluidide during summer 1984 (Fig. 5). Flurprimidol was somewhat erratic being effective two of the three years for each season. Paclobutrazol and amidochlor had consistently strong effects each spring but varied from slight to no effect between the summer and fall seasons.

The seasonal toxicity of mefluidide, amidochlor, and flurprimidol was stable across years whereas that of ethephon and paclobutrazol was variable (Fig. 6). Ethephon showed mild toxicity in summer and fall of 1984, while paclobutrazol was mildly phytotoxic during fall of 1984 and all three seasons of 1985. The divergencies in 1984 might be attributed to abnormally high temperatures during late August, September, and early October of that year.

Rooting

The chemicals had no significant effect upon root weight after treatment in 1985. Samples taken from plots treated with amidochlor, however, had consistently greatest weights among treatments 17 days after application and consistently lowest weights among treatments 51

Figure 5. Comparison by year of mean seasonal turf canopy heights in a 47 day period after growth retardant treatments. The LSD is among treatments within a season and year

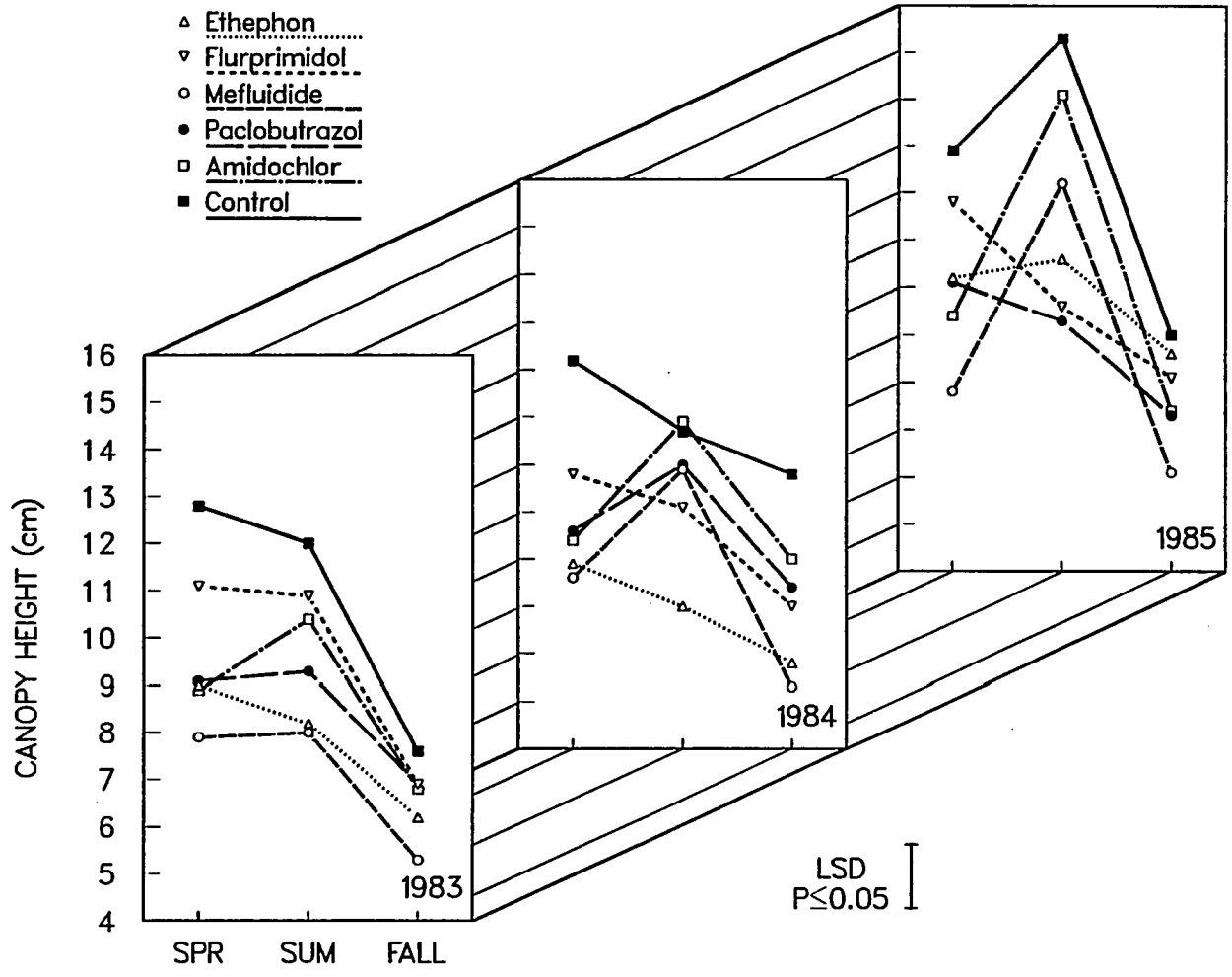

Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control
CANOPY HEIGHT (cm)
16
15
14
13
12
11
10
9
8
7
6
5
4
SPR
SUM
FALL
1983
1984
1985
LSD
P≤0.05

Figure 6. Comparison by year of mean seasonal turf quality ratings in a 47 day period after growth retardant treatments. The LSD is among treatments within a season and year

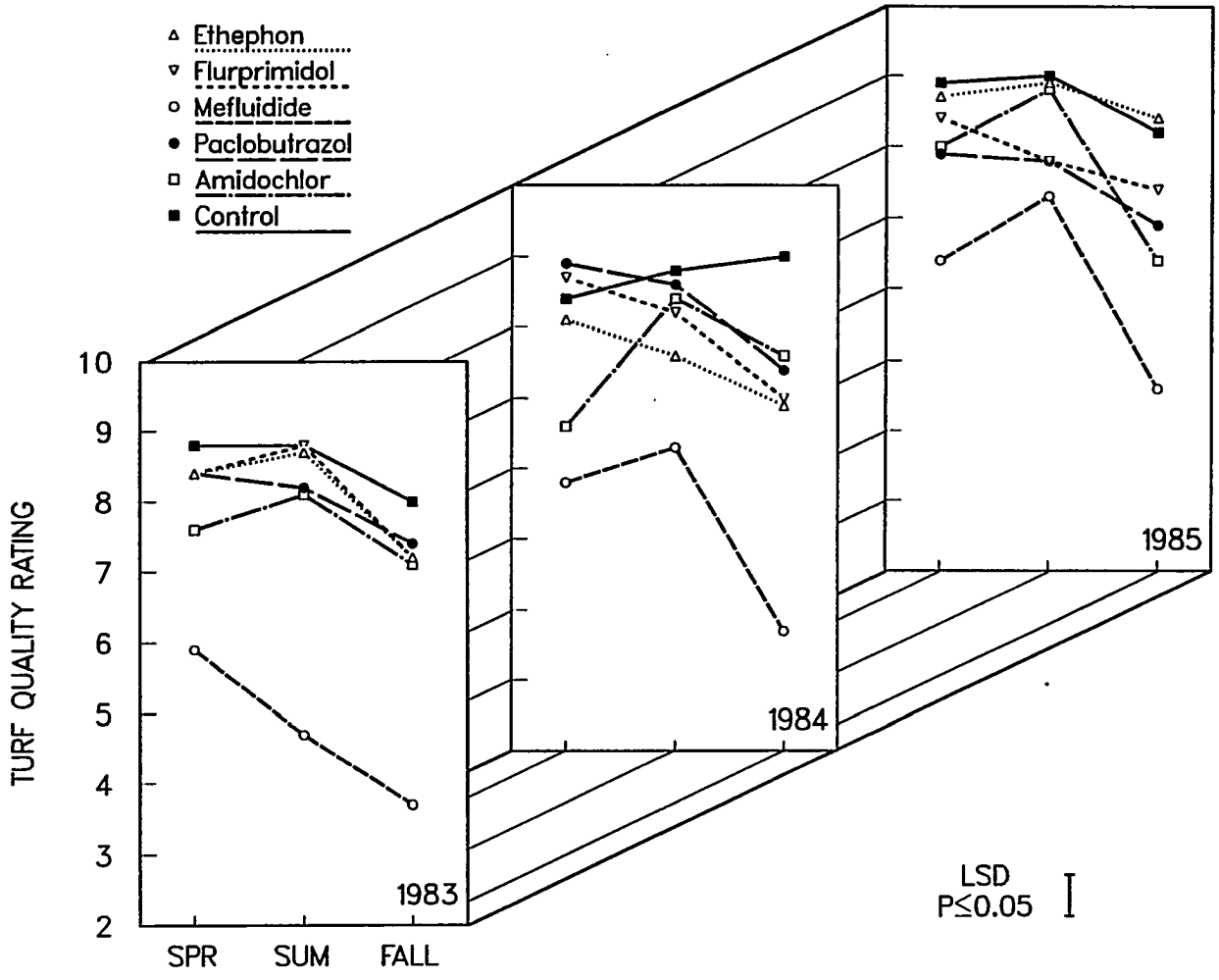

Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control
TURF QUALITY RATING
10
9
8
7
6
5
4
3
2
SPR
SUM
FALL
1983
1984
1985
LSD
P≤0.05

Table 2. Root organic matter production from five random cores per plot in response to growth retardant treatment during summer, 1985

Treatment	Days After Treatment	
	17	51
	g	
Ethephon	0.80	0.95
Flurprimidol	0.83	1.05
Mefluidide	0.81	1.02
Paclobutrazol	0.76	1.20
Amidochlor	1.12	0.62
Control	0.72	0.51
LSD[a]	0.57	0.51

[a]Significant at the 0.05 propability level.

days after application (Table 2). Since amidochlor abruptly stops leaf growth without severe plant injury, an increase in root growth due to a shift in assimilate partitioning could occur. A strong recovery from leaf growth inhibition would require root assimilates, thus causing a subsequent decrease in root volume. Kretzmer and Kaufman (34) also have found lower root weights eight weeks after amidochlor treatment.

Reports of root growth response to retardant treatments have been variable. Breuninger (5) and Elkins et al. (21) recorded limited root growth after mefluidide treatment. Dernoeden (13) obtained greater root growth from flurprimidol treatment. Christians (10), Wakefield and Fales (66), and Freeborg and Daniel (29) observed variable root growth response from ethephon treatment.

Heading

Mefluidide completely prevented heading after spring treatment while heading in plots treated with amidochlor was 21% of the control. Heading in plots treated with the other three chemicals were not different from the control. Relative levels of heading among the chemicals did not differ across years.

There is general agreement that mefluidide, when applied in spring, is an excellent preventer of seed head development. Amidochlor effectiveness varies (10, 15, 17, 30, 31, 32, 38, 61, 70). Dernoeden (13) and Buettner et al. (7) have obtained greater seed head production

than normal with flurprimidol and ethephon treatment, respectively.

Carryover Through Winter

Canopy Height and Toxicity

Ethephon was the only chemical to significantly restrict canopy growth throughout the 40-day recovery period in spring following fall treatment (Fig. 7). From 18 April to 28 May, canopy heights in ethephon-treated plots changed from 4.8 to 12.3 cm versus 6.3 to 17.6 for the other four chemicals, as a group, and 6.6 to 21.6 for the control. Ethephon showed little toxicity during that time period (Fig. 8). Mefluidide and amidochlor showed some late growth restriction on 28 May, whereas flurprimidol and paclobutrazol were even more active on that date. Plots treated with paclobutrazol and flurprimidol in fall were slower to green up the following spring but had the same turf quality ratings as the control by April 26.

Heading

Mefluidide applied each fall was as effective as spring treatment in preventing heading the following spring. Fall-applied amidochlor was not as effective as spring-applied, restricting heading to 61% of the control. Ethephon, flurprimidol, and paclobutrazol were not different from the control.

All chemicals performed similarly across years except amidochlor.

Figure 7. Spring turf growth recovery from winter after fall treatment with retardants

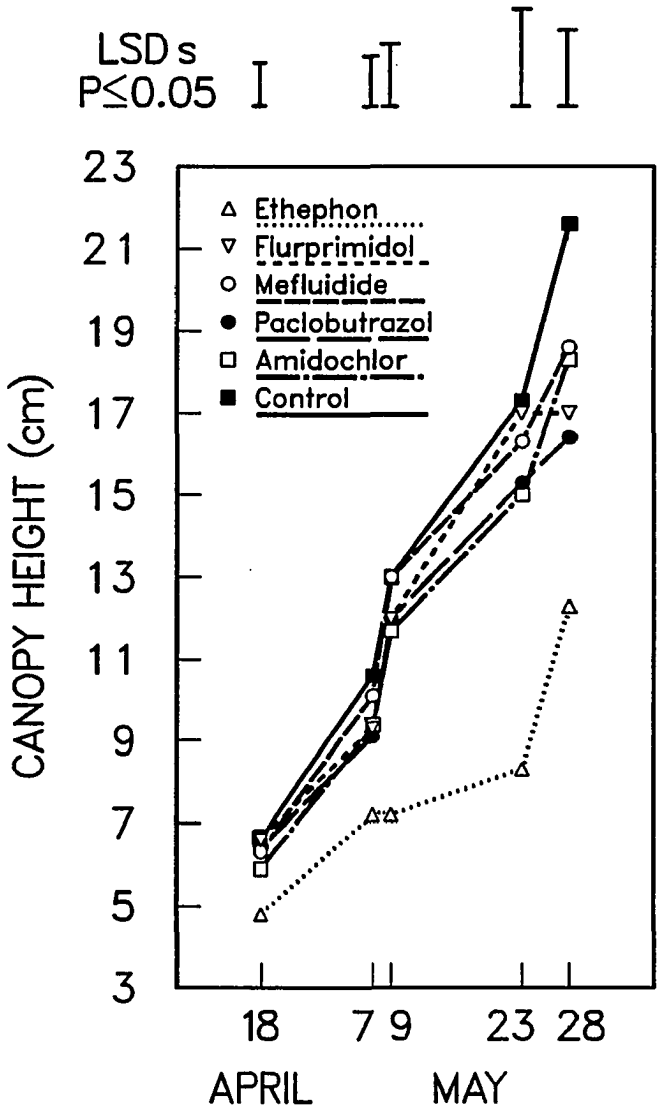
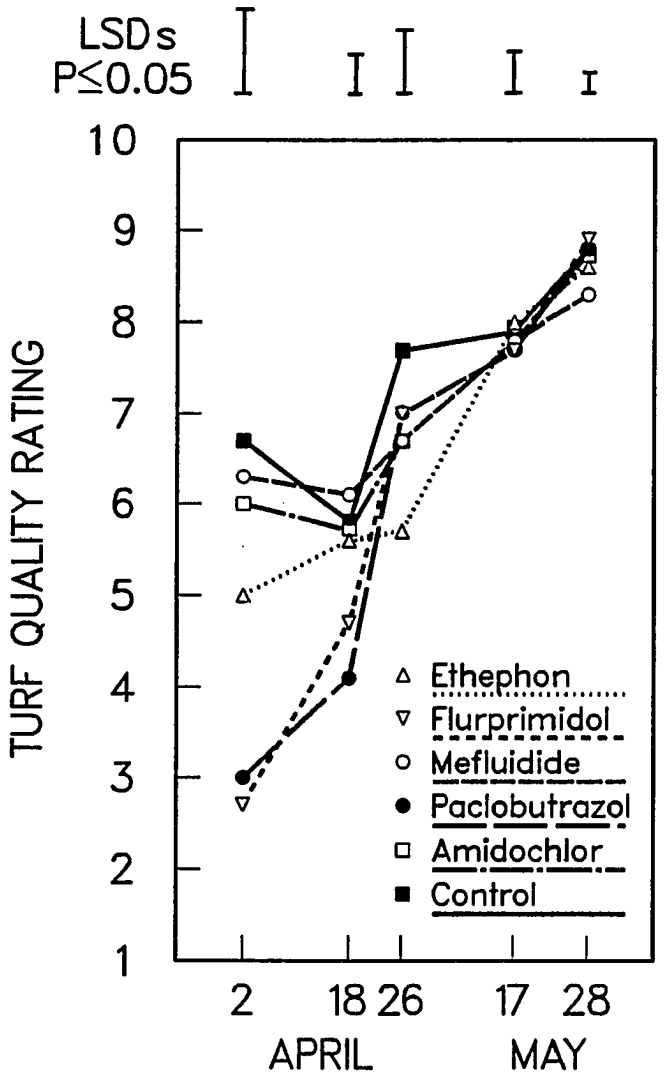

LSD s
P≤0.05
I
II
I I
23
21
19
17
15
13
11
9
7
5
3
CANOPY HEIGHT (cm)
Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control
18
7 9
23 28
APRIL
MAY

Figure 8. Spring turf quality recovery from winter after fall treatment with growth retardants


LSDs
P≤0.05
TURF QUALITY RATING
10
9
8
7
6
5
4
3
2
1
2
18
26
17
28
APRIL
MAY
Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control

After fall treatment, 1985, it completely controlled heading as did mefluidide. This is probably due to the arrival of freezing temperatures one month earlier than normal in 1985. The plants did not have enough time to induce new reproductive meristems in recovering from the mild toxicity of amidochlor.

The effectiveness of mefluidide in controlling heading would be valuable in roadside management. Treatment in fall could avert the difficulty in spraying such large areas in spring before heading has developed too far.

Blade and Sheath Lengths

Blade lengths averaged over all seasons and treatments were 15% shorter in 1984 than in 1983 or 1985, while sheath lengths were similar among years. The chemicals, as a group averaged over years, restricted blade and sheath elongation most in spring at 57 and 68% of the control, respectively, compared to 73 and 78% in summer, and 69 and 78% in fall. Differences among seasons were similar across years. The chemicals were similar among years in their degree of growth restriction but they varied across seasons.

Four Weeks After Treatment

Ethephon, mefluidide, and amidochlor caused the shortest blade lengths four weeks after all three application dates while flurprimidol

and paclobutrazol were less effective (Fig. 9). Amidochlor performed as well as ethephon and mefluidide in spring but was among the least effective treatments in summer and fall. Ethephon, flurprimidol, mefluidide, and paclobutrazol were comparable in restricting sheath elongation four weeks after each seasonal treatment (Fig. 10). Their degree of restriction was greatest in spring. Amidochlor had the least effect on sheath growth in spring and fall and no effect in summer.

Six Weeks After Treatment

Ethephon was the strongest blade growth inhibitor six weeks after all application dates (Fig. 9). Mefluidide effects had diminished during spring and summer but remained as strong as those of ethephon in fall. Amidochlor effects also diminished in spring along with those of mefluidide becoming equal to those of paclobutrazol. Flurprimidol effects were absent across all seasons at this time as were those of paclobutrazol and amidochlor in summer and fall. Ethephon was the only chemical to strongly restrict sheath growth six weeks after all three treatments (Fig. 10). Sheath lengths of the other four chemicals varied so greatly across seasons that none could be determined as different from the control.

Figure 9. Mean seasonal blade lengths of shoots sampled 4 and 6 weeks after growth retardant treatments, averaged over years. The LSD is among treatments within a season

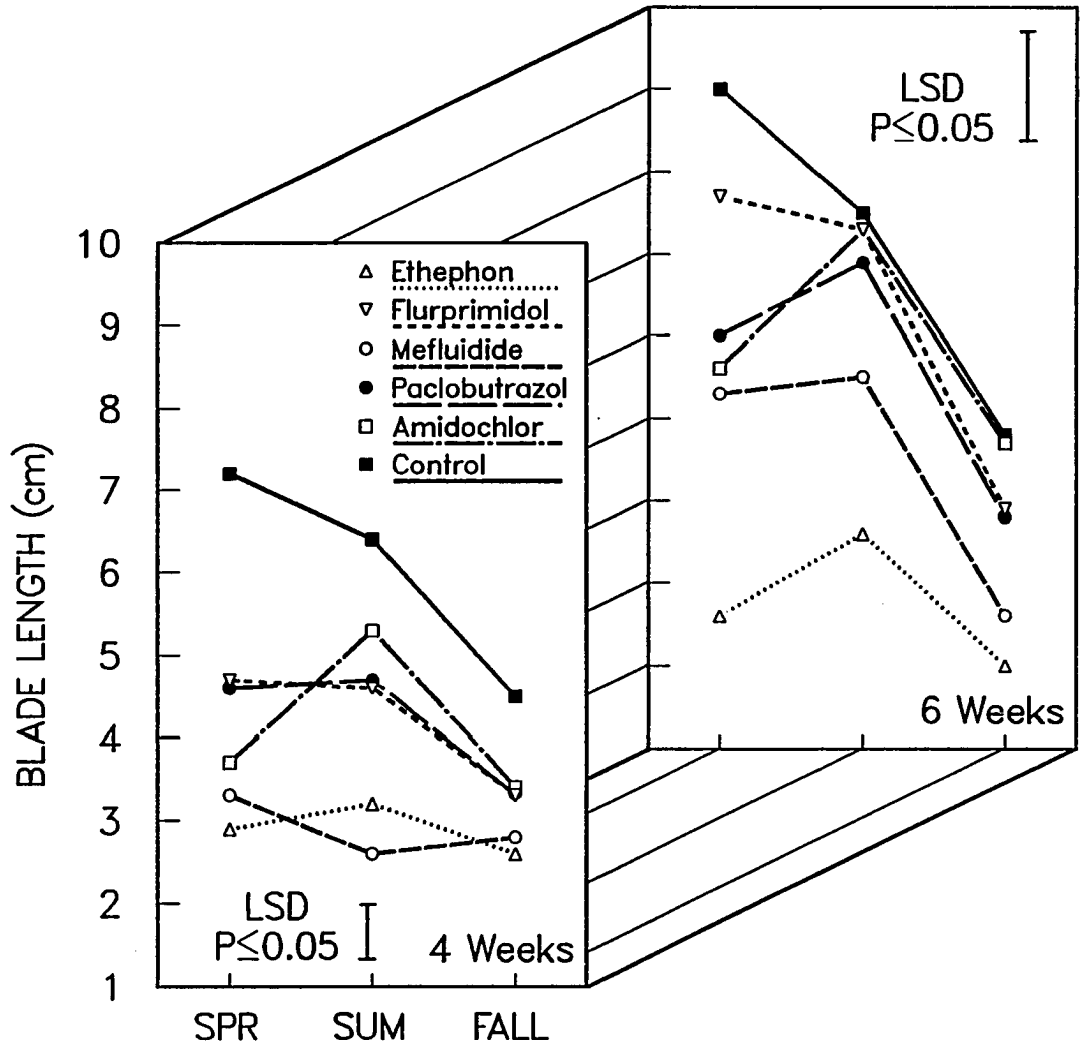
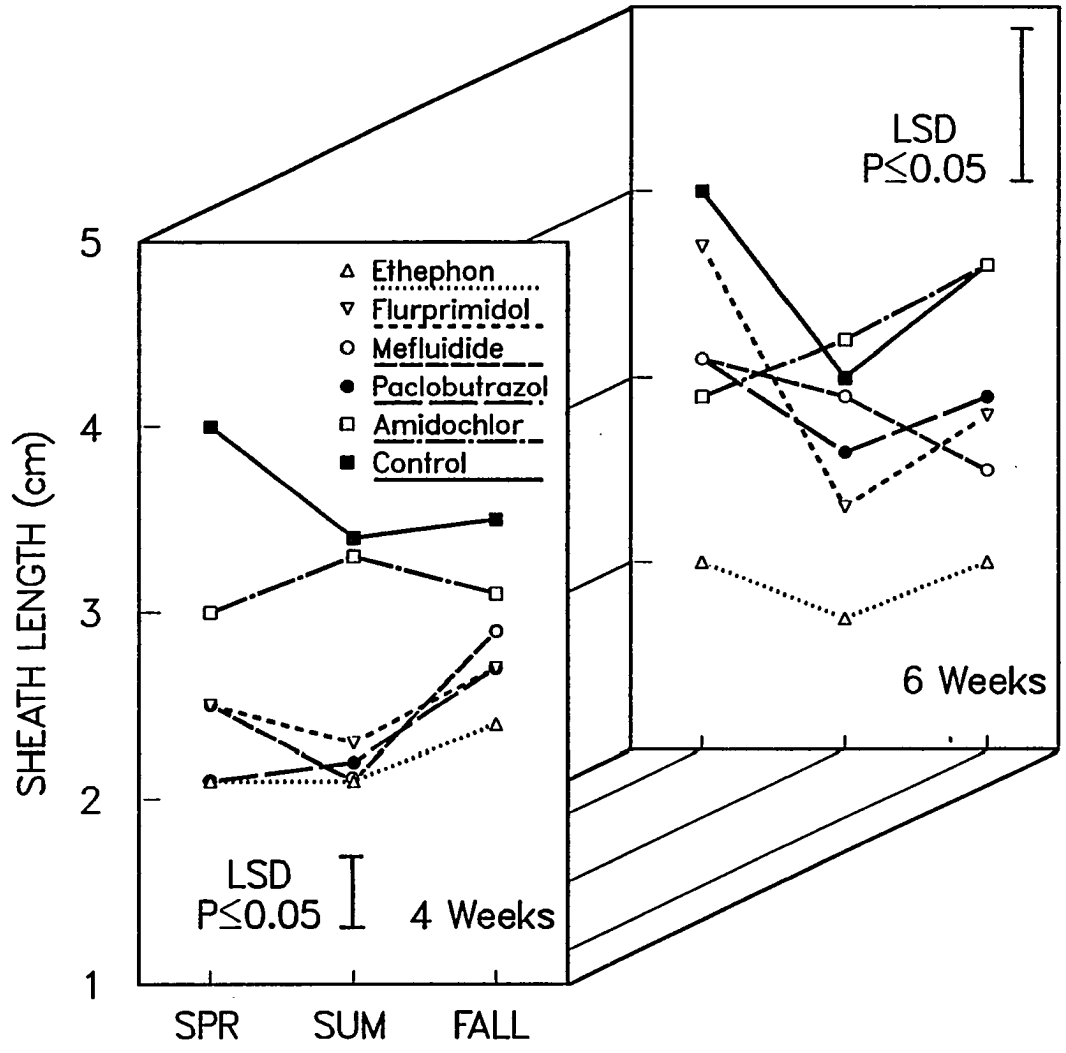

BLADE LENGTH (cm)
10
9
8
7
6
5
4
3
2
1
SPR
SUM
FALL
Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control
LSD
P≤0.05
4 Weeks
LSD
P≤0.05
6 Weeks

Figure 10. Mean seasonal sheath lengths of shoots sampled 4 and 6 weeks after growth retardant treatments, averaged over years. The LSD is among treatments within a season


SHEATH LENGTH (cm)
5
4
3
2
1
SPR
SUM
FALL
Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control
LSD
P≤0.05
4 Weeks
LSD
P≤0.05
6 Weeks

Phytomers

The effects of a growth regulator on shoot growth over time can be seen more clearly by noting plant response in successive phytomer development. With three to four healthy phytomers per shoot, each phytomer represents a block in time, perhaps 7 to 14 days, overlapping those of both adjacent phytomers, encompassing altogether a four-week period. Data from the three oldest phytomers of the four-week sampling were combined with data from the three youngest phytomers of the six-week sampling to describe response to treatment over a six-week period (Fig. 11).

Ethephon consistently had the strongest effect on both blade and sheath growth at all phytomers within all seasons (Figs. 11 and 12). Paclobutrazol was usually among the strongest sheath growth inhibitors but a less effective blade growth inhibitor. Sheath and blade growth response to the other three chemicals differed among phytomers and seasons.

Ethephon and mefluidide were strong inhibitors of blade growth throughout the six weeks after each application date. However, plants were recovering from mefluidide effects during the fifth or sixth week (Fig. 11). Expression of mefluidide and ethephon effects was slower in spring and fall than in summer, becoming evident in the second blades rather than the first. In plots treated with mefluidide, 43% of the leaves had died and were absent due to phytotoxicity in the oldest phytomer. Amidochlor restriction of blade growth was similar to that of

Figure 11. Comparison by year of seasonal phytomer blade lengths in response to growth retardant treatments. LSDs 1 through 6 refer to corresponding phytomers within each season

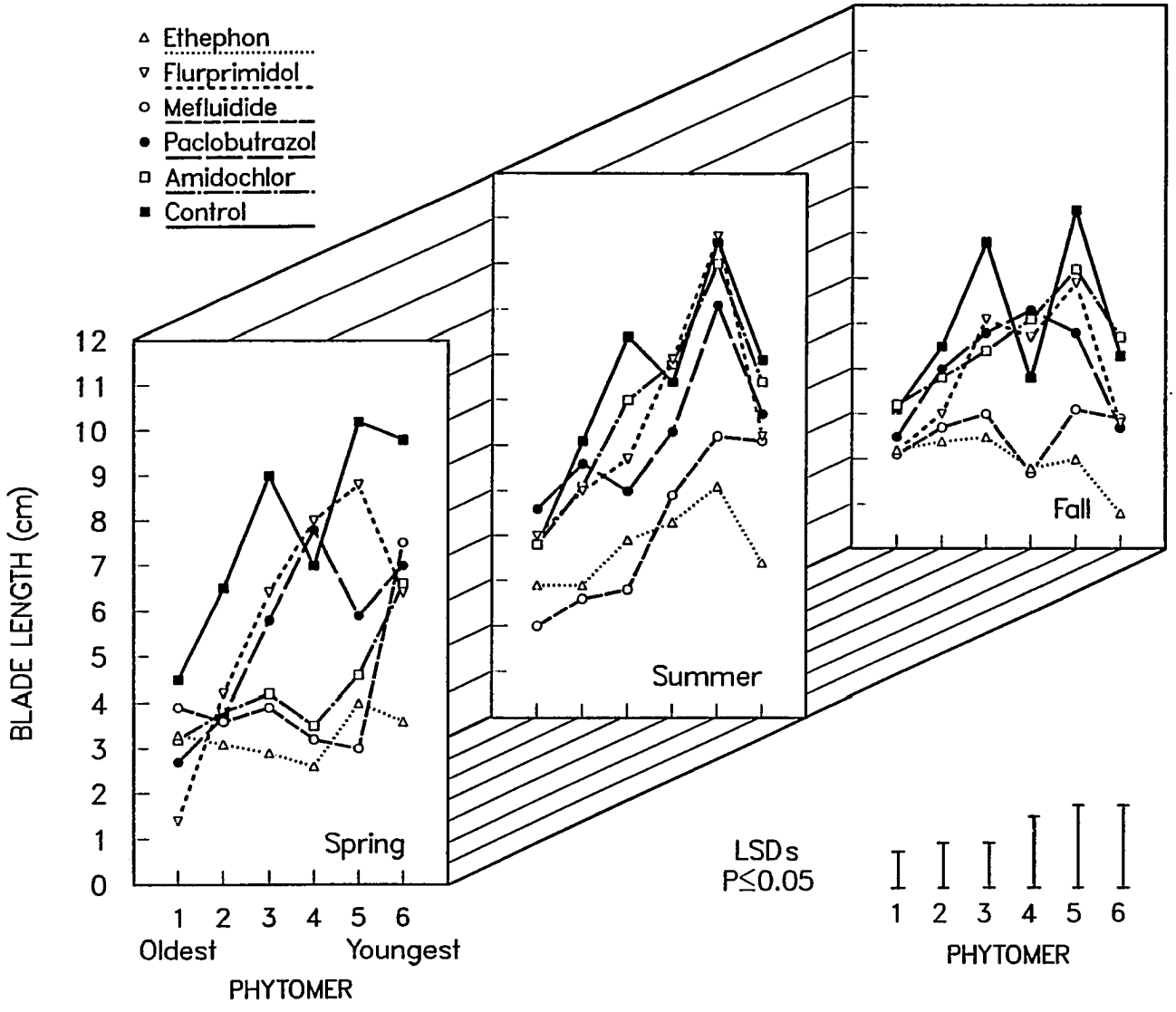
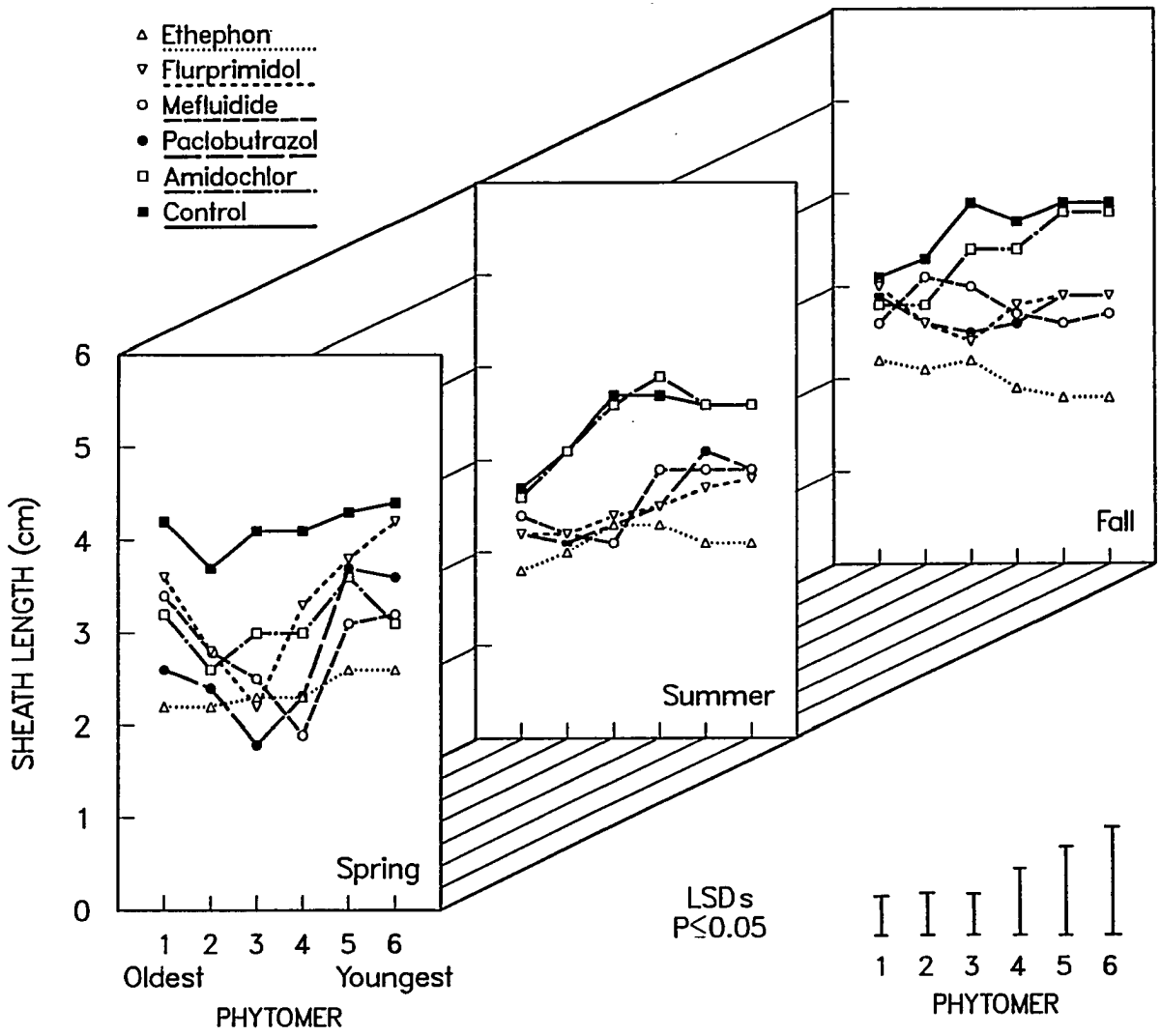

Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control
BLADE LENGTH (cm)
0
1
2
3
4
5
6
7
8
9
10
11
12
Spring
Summer
Fall
1 2 3 4 5 6
Oldest
Youngest
PHYTOMER
LSDs
P≤0.05
1 2 3 4 5 6
PHYTOMER

Figure 12. Comparison by year of seasonal phytomer sheath lengths in response to growth retardant treatments. LSDs 1 through 6 refer to corresponding phytomers within each season


Ethephon
Flurprimidol
Mefluidide
Paclobutrazol
Amidochlor
Control
SHEATH LENGTH (cm)
0
1
2
3
4
5
6
Spring
Summer
Fall
1 2 3 4 5 6
Oldest
Youngest
PHYTOMER
LSDs
P≤0.05
1 2 3 4 5 6
PHYTOMER

mefluidide during spring but without any loss of leaves. In summer and fall, however, it was virtually ineffective with the exception of inhibition of growth in the third developing leaf. Although flurprimidol and paclobutrazol averaged the same level of activity after each application date, they were the least consistent over each six-week period. In spring, flurprimidol showed the strongest restriction in blade elongation among the treatments in the first phytomer, then was comparable to paclobutrazol in blades two through four. In the fifth blade, flurprimidol was ineffective while paclobutrazol was at its peak activity and comparable to ethephon and amidochlor. In the sixth blade, flurprimidol activity resumed and was similar to that of mefluidide, paclobutrazol, and amidochlor. In summer and fall, flurprimidol was active in the second and third blades, inactive in blades four and five, then resumed activity in blade six. Paclobutrazol in fall was active in blades three through six with the exception of blade four.

Sheath growth response to treatments was different from blade growth response (Fig. 12). Ethephon inhibited sheath growth the most in all three seasons. Additionally, it allowed sheath lengths to vary the least across phytomers and seasons, ranging from 1.8 to 2.6 cm. In spring and fall, effects of the other chemicals varied among phytomers. Ethephon and paclobutrazol were the strongest inhibitors during spring in sheaths one through four, whereas ethephon and mefluidide inhibited sheath growth the most in phytomers four through six. Flurprimidol and amidochlor were least effective in spring except in the third and sixth phytomers, respectively. In summer, amidochlor was completely

ineffective while the other four were comparable across phytomers. In fall ethephon was most effective while flurprimidol and paclobutrazol were second and joined by mefluidide in sheaths four, five, and six. Amidochlor was the least effective in sheaths two and three and ineffective in the last three sheaths.

Internode Elongation

Ethephon-treated plants always had elongated internodes, whereas the other chemicals occasionally caused internode elongation (Table 3). Differences in average internode length were not significant. Average and total internode lengths for the chemical treatments, as a group, were not significantly different among seasons, although measurements were consistently smaller in spring than in summer or fall.

Table 3. Phytomer internode frequency and length six weeks after treatment, averaged over seasons and years

Treatment	Phytomer 1 Oldest	2	3	4	5	6	7	8 Youngest
	cm (n^a)							
Ethephon	0.3 (36)	0.6 (36)	0.7 (30)	0.5 (17)	0.4 (5)	0.3 (2)	0.5 (2)	0.3 (1)
Flurprimidol	0.2 (2)	0.2 (2)	0.2 (1)					
Mefluidide	0.2 (4)	0.2 (4)	0.2 (4)	0.4 (1)				
Paclobutrazol		0.2 (2)						
Amidochlor	0.2 (6)	0.3 (1)						
Control	none							

[a]n=number of internodes contributing to the mean.

DISCUSSION

The data from this study demonstrate the variable seasonal responses of Kentucky bluegrass to the five growth retardants. Effects of the chemicals on canopy height and blade length relative to the control differed most between spring and summer (Figs. 3 and 9). Spring and summer represent the reproductive and vegetative growth phases, respectively. Amidochlor and mefluidide were more effective in the reproductive phase while flurprimidol was more effective in the vegetative phase. Ethephon and paclobutrazol effectiveness were similar in both phases. These seasonal effects were consistent among years, although there were exceptions when a chemical would act either more strongly or rapidly in a season of one year compared to the other two years (Figs. 5 and 6). This could have been due to transient environmental conditions such as ideal soil moisture, relative humidity, cloud cover, or diurnal temperatures, favoring rapid assimilation of the compounds. The restriction on blade growth by each growth retardant was remarkably steady across phytomers. This corroborates the consistent seasonal effects of the chemicals across years. Neither weekly fluctuation in climate nor yearly climatic variations altered their effects significantly. The consistent differences in seasonal plant response to treatments in spite of yearly climate variations supports the hypothesis that the unique combinations of season with growth phase influence the response of Kentucky bluegrass to turf growth retardants.

These data can partially explain why response to growth regulator

treatment is inconsistent. The change in Kentucky bluegrass from reproductive to vegetative growth in spring is rapid. In less than a month, heads expand, extrude, and set seed. The shoots supporting them die as the seeds ripen and new vegetative tillers take over the life of each plant (24). Turf managers applying growth retardants at different times during this transition could obtain highly variable results. Changes in diurnal or daily temperatures can add to the variability.

The reason Kentucky bluegrass reacts differently to each retardant could be explained in the chemicals' mode of action if more were known. This is the area where the greatest emphasis in future research should be placed. In the case of ethephon, Biddle et al. (4) have shown that its rate of ethylene generation depends strongly upon pH, while other researchers (35, 45) have demonstrated the significant role of temperature at a given pH. Ethephon releases ethylene as it decomposes in plant tissue (12, 26, 40, 67, 74), and is considered a true growth regulator, not a retardant (14). Van Andel (64) found that ethephon inhibits cell division in Kentucky bluegrass leaves while Ridge and Osborne (51) determined that it inhibited cell elongation, as well. Ethylene is generally thought to inhibit growth (8, 41, 50, 53) but there are cases, as with Kentucky bluegrass internode elongation, where it is associated with growth stimulation (42, 46, 52, 55, 58, 63, 64). Pratt and Goeschl (50) demonstrated that internode elongation in culm development of Kentucky bluegrass is generally associated with shorter leaves. Mefluidide interferes with cell division in the stem apex (9, 55). Amidochlor activity could be similar to that of mefluidide since

their effects on turf are similar, disregarding their relative toxicities. Flurprimidol and paclobutrazol are thought to interfere with the biosynthetic precursors of the growth-stimulating gibberellins (14). Regulation of turf growth by this type of material has proven to be dissatisfactory because of variable growth suppression and lack of persistence (6).

Plant metabolic rate seems to be a strong factor in the effectiveness of the slow (flurprimidol and paclobutrazol) and continuous acting (ethephon) chemicals. In mid-spring and summer, they are more active when plant metabolism is high, but in fall it is so low that these growth regulators lack sufficient time to have a major effect on plant growth before winter sets in. Effectiveness of the fast acting chemicals (mefluidide and amidochlor) seems to be related to the ability of treated plants to recover from phytotoxic shock or to grow new tillers after the existing ones are completely prevented from growing. In spring this is especially difficult because most of the plant energy is devoted to seed head production and very few expanded axillary buds or immature tillers exist. Most recuperation of growth must come from pre-existing shoots or the breaking of axillary buds from dormancy and subsequent growth, which can take more than five weeks, depending upon growth conditions (24). Kretzmer and Kaufman (34) have shown that the toxicity of amidochlor is slight enough to allow renewal of growth in pre-existing shoots. In summer, many axillary buds have expanded and recovery is more rapid. In fall there are many young tillers emerging from the ground which can more quickly recoup any loss of growth

inflicted on existing, mature tillers. If temperatures become too cold, however, these young plants take longer to grow the new leaves that would block visibility of discoloration in the older shoots.

Blade growth was the greater determinant of canopy height in response to growth retardant treatments as evidenced by the superior effectiveness of mefluidide which strongly affected blade length but did not affect sheath length any more than the other chemicals. Amidochlor, likewise, had little effect on sheath growth but restricted canopy growth in spring almost as well as mefluidide through blade growth inhibition. In corollary, the weak effect of paclobutrazol upon blade growth prevented its overall effectiveness, even though it had a strong effect upon sheath growth. Ethephon had a strong effect upon both sheaths and blades, but it also stimulated internode elongation which raised canopy height. Even so, it restricted overall canopy height as well as mefluidide over the six-week periods. Canopy height over all treatments was positively correlated with blade and sheath length at R=0.66** and 0.37**, respectively. Van Andel (63, 64) has also found a stronger response to ethephon in blades over sheaths.

Blade growth was more sensitive to the seasonal application dates than sheath growth. Figure 3 shows that canopy height dropped in the treated plots from summer to fall similarly to that in the control plots. A similar drop in all plots is shown for blade lengths (Fig. 9) but not sheath lengths (Fig. 10). The lack of a decrease in sheath growth in fall could be due to a change in the partitioning of assimilates in winter hardening. The leaf sheath is known to be

involved in carbohydrate storage in perennial grasses (1, 26, 38, 60).

Plant growth response to treatments is usually reported on the basis of a net change in dimension, volume, or weight over a predetermined period of time. It is valuable to know in what manner the net change occurred. It could have started or finished rapidly or slowly, or the weight could have fluctuated instead of changing steadily in one direction. Repeated measurement over shorter time periods can answer these questions, but the monumental resource commitment in data collection and analysis usually prevents the effort. The value in measuring phytomer development in a vegetative perennial grass is that each phytomer is like a "subplant" representing a small block in time and expressing the same category of vegetative growth response to a treatment. The phytomer blade and sheath data in this experiment indicate two trends: (1) blade growth appears to be more sensitive to retardant treatment than sheath growth, and (2) the time periods in which response to treatment occurred varied among retardants.

In researching mode of action it is important to know which plant parts are being most affected. This study was a beginning in that direction by looking at canopy height in terms of blade, sheath, and internode length. The next logical step is to subdivide those parts into regions of response. Verkerke and van Andel (65) have already found two distinct regions in some Kentucky bluegrass internodes in response to ethephon treatment. Information like this can then be correlated with physiological data regarding hormones, RNA, 2nd messengers, proteins/enzymes, or control point intermediates. With

enough of this kind of information, cause and effect scenarios and, eventually, complete chemical pathways could be determined. Chemists armed with this new information could then begin the development of what can be called 'surgical chemicals' which affect specific control points in pathways, thereby targeting one plant species, subspecies, or even cultivar, and minimizing further environmental impact. From a plant breeder's viewpoint this knowledge could be used to identify key physiologic components for isolation through traditional breeding methods and new gene-splicing techniques.

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PAPER II. AN EASY-TO-BUILD CONTINUOUS AIR EXCHANGE ROOMETTE AND GAS METING SYSTEM

An easy-to-build continuous air exchange roomette and gas meting system[1]

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[1]Contribution from the Department of Horticulture, Iowa State University. Published as Journal Paper No. J- of the Iowa Agriculture and Home Economics Experiment Station, Ames, IA. Project 2232.

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ABSTRACT

A continuous flow system with portable roomettes and precise control of air and ethylene was constructed from materials common to most laboratories. Desiccators were used as roomettes to expose hydroponically grown Kentucky bluegrass (Poa pratensis L.) plants to ethylene concentrations of 10 to 3000 µL/L for up to eight days. Influx of ethylene into 1.0 or 3.6 L/min air flow was controlled with 0.152-mm bore capillary tubes of appropriate lengths with a constant pressure head regulated by a barostat tower. Air flow was similarly controlled with 1.0-mm x 2.3-cm capillary tubes and separate barostat tower.

Near-normal growing conditions can be maintained. Air is exchanged once every eight minutes inside the desiccators. This prevents high temperatures and moisture condensation while replenishing CO_2. A stirring magnet at the bottom of each roomette adds to air turbulence. Roomette temperature and irradiance are subject to ambient conditions deviating from the mean 15 and 18%, respectively. Relative humidity is maintained at 85 $\pm$ 8% with humidifying stacks. Coalescing filters and molecular sieve 4A (8-12 mesh alumina silicate/sodium) eliminate compressor oil and random ethylene, respectively, from the air supply.

Additional Index Words: controlled atmosphere, growth chamber

INTRODUCTION

The most difficult conditions to manipulate in controlled environments are those associated with the atmosphere. Plants must be at near-optimal growth which requires constant air exchange to maintain steady-state gas concentrations with ample optimal irradiance, water, and nutrition. Once this is accomplished, precise control of air component gas concentrations can result in accurate assessment of their effects on plant growth. Some excellent gas-meting apparatus (2, 5, 12, 17, 19) and transparent roomettes (1, 3, 6, 21) have been devised. There is only one report (3) of a complete, continuous-flow, gas-meting and roomette system. The roomettes described in that report are complex and custom-built, though less expensive than growth chambers, and the gas-meting system is designed for large-volume flow. This paper describes such a system that can be built more inexpensively from materials common to most laboratories. A full range of gas concentrations can be accurately and precisely controlled while allowing optimal irradiance, temperature, humidity and nutrition.

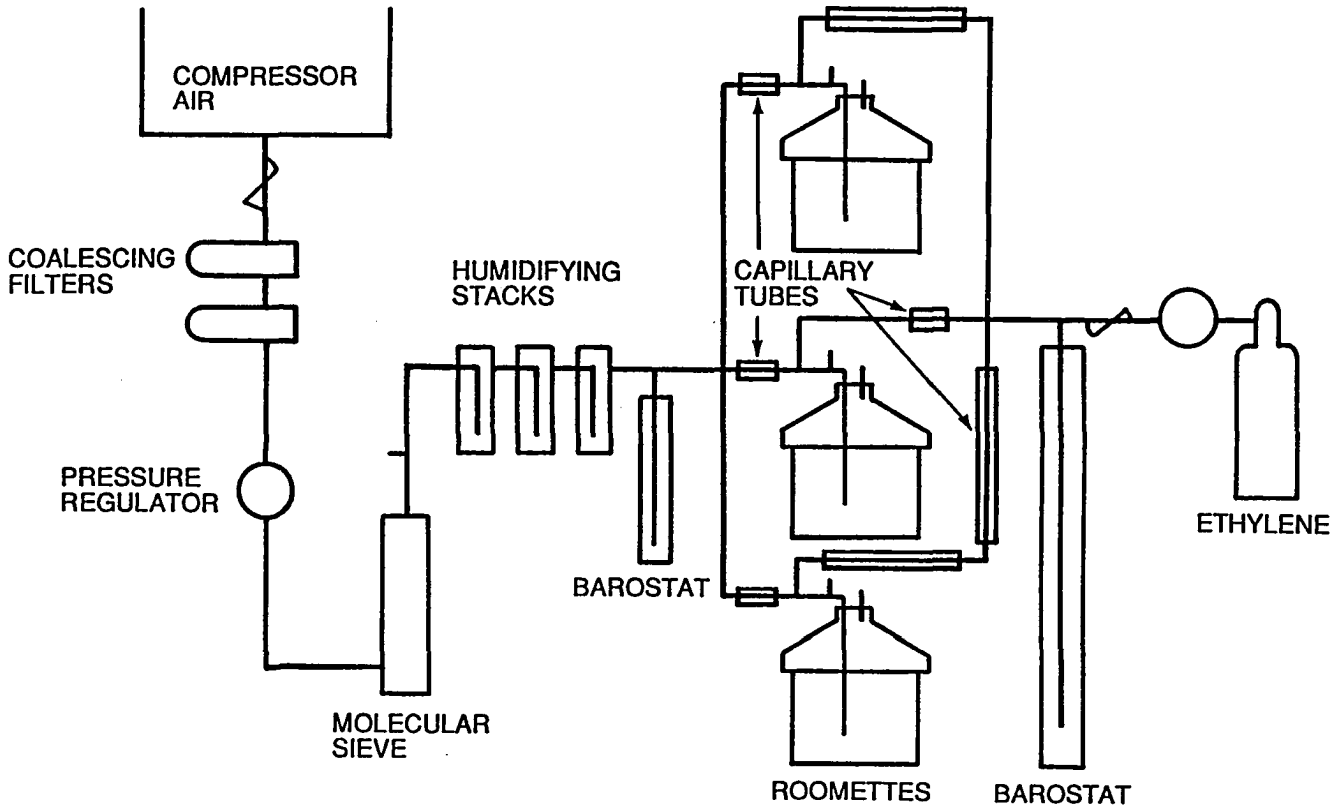
MATERIALS AND METHODS

The gas-meting portion of the system (Fig 1) is designed after the same principles as those of Ahmad (2) and Morris (12) with the exception that both authors relied upon pressurized gas tanks to supply their systems. This limits experiments to either slow flow rates for long-term treatment or short-term treatment at higher flow rates for an adequate carbon fixation rate from CO_2. Portability is also limited by the necessity for the many, large, pressurized tanks.

Air Supply

Air from laboratory bench ports was transferred to system components via 5- and 6-mm inside diameter (id) glass and stainless steel tubing with tygon tubing connections. Air pressure regulated at 8.3×10^4 Pa was sufficient to supply the system without bursting the lines or components. Oil droplets from the university compressors were removed with two Balston A92 coalescing filters (Balston, Inc., 703 Massachusetts Ave., Box C, Lexington, Massachusetts 02173). The first, grade DX, is 93% efficient for 0.1 micron particles and droplets while the second, grade BX, is 99.99% efficient. Random ethylene was removed as air passed through a column of molecular sieve 4A (8-12 mesh alumina silicate/sodium). Three humidifying stacks were used to maintain relative humidity at $85 \pm 8\%$. Constant pressure and flow rate to each roomette was controlled by a barostat tower before the manifold, and capillary tubes of equal diameter and length after the manifold and

Figure 1. Schematic drawing of the continuous flow roomette and gas-meting system. The number of roomettes can be varied as needed


COMPRESSOR AIR
COALESCING FILTERS
PRESSURE REGULATOR
MOLECULAR SIEVE
HUMIDIFYING STACKS
BAROSTAT
CAPILLARY TUBES
ROOMETTES
BAROSTAT
ETHYLENE

equidistant from their respective roomettes. Experimental treatments required 3, 5, or 7 roomettes. Capillary tubes 2.3 cm x 1.0 mm bore created enough pressure head to allow adjustment of air flow rates of 1.0 to 3.6 L/min by changing the barostat tower air-column depth.

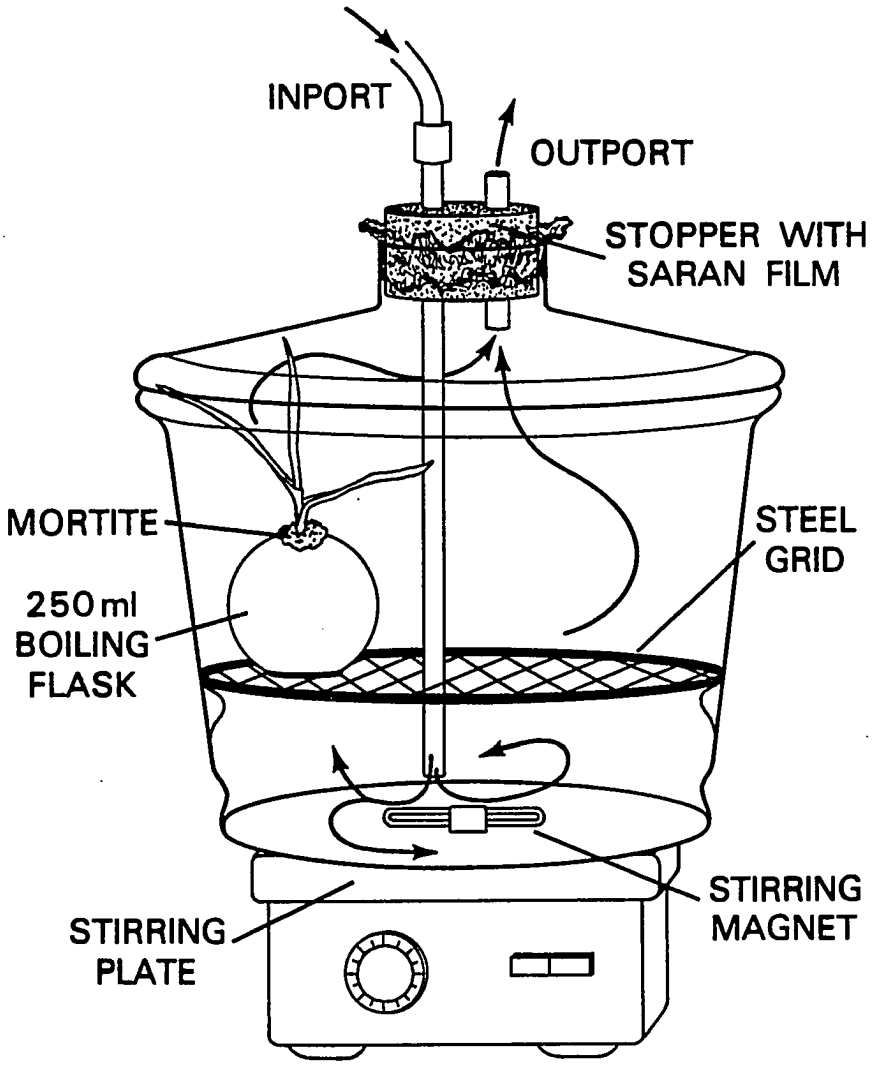
Roomettes

The exposure chambers (roomettes) were 9.2-L desiccators with the top of each lid removed allowing installation of ports with glass tubing held by neoprene cork wrapped in Saran film (Fig 2). The inport extended to the bottom forcing the air to travel through the roomette before it passed through the outport at the top. Air turbulence inside each roomette was created with a 7.5-cm stirring magnet rotated by a stirring plate positioned under the roomette. The ceramic plate which is usually inside a desiccator was replaced with a 2.5-cm mesh galvanized, steel, wire grid to allow free air flow around the plant containers supported by the grid.

Ethylene Supply

Pressurized pure or diluted ethylene was supplied to each roomette through a sequence of pressure regulator, barostat tower and capillary tubes similar to that of the air supply. Connection to the air supply line must be at some point between the air supply capillary tube and its respective roomette. A sampling port with white rubber septum is placed in the line immediately prior to the inport of each roomette and at least 25 cm away from the ethylene connection to allow thorough mixing

Figure 2. A 9.2-L desiccator used as a roomette with ports for continuous air flow and a stirring magnet and plate supplying additional turbulence


INPORT
OUTPORT
STOPPER WITH
SARAN FILM
MORTITE
250 ml
BOILING
FLASK
STEEL
GRID
STIRRING
MAGNET
STIRRING
PLATE

of gases.

An important difference between the ethylene and air supply lines is in their capillary tube bore diameter, 0.152 versus 1.0 mm, respectively. The extremely small diameter enables treatment with ethylene at less than 10 µL/L. They vary in length according to the concentration of ethylene needed in each roomette. A variation of the Hagen-Poiseuille Formula

$$Q = \frac{\pi B \Delta P D^4}{128 u L}$$

(Dr. Alfred Joensen, Mechanical Engineering Department, Iowa State University, personal communication) was derived from Poiseuille's Law (13). Capillary tube length can be determined where Q=flow rate (cm^3/sec), B=barostat air-column depth (cm), ΔP=change in pressure per cm of barostat air-column depth (980 dynes/cm^2), D=capillary tube bore diameter (cm), u=gas viscosity (g/cm sec), and L=capillary tube length (cm). Capillary tube length becomes prohibitively long for treatment levels less than 100 µL/L, so pure ethylene must be diluted into a pressurized tank. Saltveit and Dilley (20) explain how this can be easily done by mixing pressurized pure ethylene and air while pressurizing a third container.

Ethylene concentrations of 10, 27, 100, 670, 1000, and 3000 µL/L were applied. When ambient temperatures were stable, as in a laboratory or growth chamber, the standard deviation of ethylene concentration was 4% of the mean. One experiment was conducted in a greenhouse where

ambient diurnal temperatures fluctuated between 18 and 24 C. These temperature fluctuations increased the standard deviation to 11% of the mean.

Plant Containers

Five 250-ml boiling flasks with necks removed were placed in each roomette. Shoots of a vegetatively propagated Kentucky bluegrass clone were held at the top of each flask with Mortite (Mortell Company, P.O. Box 71, 550 N. Hobbie Ave., Kankakee, Illinois 60901). The plants were grown in a greenhouse in Hoagland (11) solution modified for turf (15). The flasks were double-wrapped with aluminum foil to insulate them and to block light from the roots. The solution in each flask was aerated from an air pump via a 2-cm id polyethylene manifold and 1.0-mm id polyethylene tubing. Shoots were transported to the roomettes at the two- to three-leaf stage. Shoots were treated ten days with no apparent growth deficiency. After treatment they were returned to the greenhouse and aeration of fresh nutrient solution was resumed. With the exception of the treatment period, nutrient solution was changed every 3 to 7 days, depending on the size of the plants, with smaller plants placing less demand on solution nutrients. Use of hydroponics allows repeated, nondestructive measurement of root as well as shoot weight and dimensions over time. Roots were weighed using a water displacement technique (7, 24) based on Archimedes' principle of buoyancy.

DISCUSSION

Contamination can be a problem in experiments requiring low test concentrations of ethylene. The molecular sieve eliminates ethylene coming from external sources (8). Gas chromatographic analysis of air samples taken from a container of Mortite sealed for 4 hours detected 0.01 μL/L ethylene; that is an evolution rate of 0.025 μL/L hr as compared to laboratory room air containing 0.84 ± 0.33 μL/L ethylene. Mortite is a highly impervious, pliable compound that is nontoxic to plants (10, 22) and can be found in most home improvement stores. The only remaining sources of ethylene in the gas-meting and roomette system release extremely low levels: finger prints at 5×10^{-4} μL/m^2 hr (6), vacuum grease at 2×10^{-4} μL/g hr (6), Saran film, which is highly impermeable to gases (16, 18), and possibly the plastic-covered stirring magnets. Tygon tubing and white rubber septa are permeable to ethylene at 3×10^{4} and 102 μL/m^2 hr, respectively (14, 19). These figures were obtained from ethylene gradients of 100 and 0.01% across the respective materials. The ethylene gradient across any material previous to ethylene influx in this system averaged 8×10^{-5}%, and all ethylene treatment concentrations were higher inside the system, so ethylene diffusion was outward. Neither condition, therefore, would alter ethylene treatment levels. Surface exposure of the vacuum grease and tygon tubing were minimized by fitting the glass together as tightly as possible. Additionally, the flow rate of 1 L/min quickly carried each ethylene molecule away as soon as it was released. Samples taken distal

to the molecular sieve and proximal to ethylene influx and analyzed in a gas chromatograph contained 0.07 $\pm$ 0.05 μL/L ethylene. Samples taken from control roomettes with untreated plants contained 0.08 $\pm$ 0.10 μL/L ethylene.

High relative humidity is necessary to prevent plant desiccation or low water potential which would inhibit plant response to treatment. The dryness of the compressor-supplied air together with the relatively high rate of flow necessitated the use of three humidifying stacks. The first one was used merely as a source of water to keep the two subsequent ones from going dry over long-term treatment, and had to be refilled every second or third day. Humidity was controlled by changing the number of humidifying stacks, air flow rate, or amount of water in the humidifying stacks distal to the first one.

Capillary tubes have the distinct advantage of allowing no variability in gas flow rate. Mechanical valves randomly come out of adjustment and require constant monitoring. A capillary tube does not act as a critical orifice through which the flow rate becomes independent after a critical pressure differential is reached. Rather, it acts as a constant resistance to air flow. The Hagen-Poiseuille Formula shows that the flow rate is inversely proportional to the capillary tube length, directly proportional to the barostat air column depth and proportional to the fourth power of the capillary tube diameter. Thus, after the proper capillary tube diameter was determined, the flow rate was precisely set by adjusting either the capillary tube length or the barostat air-column depth.

The desiccators add valuable flexibility to the treatment system. Desiccators come in standard sizes, so the number of treatments is not limited by the supply of expensive, custom built roomettes. Portability of the system is another asset. Irradiance control is limited only by the outside facilities to which the system is moved. Irradiance levels inside the desiccators averaged 82% of ambient levels. The air flow of 1 L/min through the 9.2 liter roomettes (minus the 1.25 L occupied by the plant containers) resulted in one air exchange every 8 minutes. This relatively rapid air movement not only was a constant replenishment of CO_2 for optimum carbon fixation (4, 9, 23) it also prevented moisture condensation on the inside surfaces of the roomettes. Inside temperatures were close to ambience as long as the air-supply temperature is not radically different from ambience. Such a difference is unlikely in large air-supply systems where the air is piped through underground tunnels or inside buildings, thereby insulated from temperature extremes. Midday sun irradiance in a greenhouse during a clear April day raised roomette temperature only 3 C in 23 C ambience or 13% above the greenhouse temperature. On cloudy days or under netting there was no temperature difference observed.

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PAPER III. INDEPENDENT AND INTERACTIVE EFFECTS OF ETHEPHON AND ETHYLENE ON KENTUCKY BLUEGRASS (*POA PRATENSIS* L.) MORPHOGENESIS

Independent and interactive effects of ethephon and ethylene on Kentucky bluegrass (*Poa pratensis* L.) morphogenesis[1]

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[1]Contribution from the Department of Horticulture, Iowa State University. Published as Journal Paper No J- of the Iowa Agriculture and Home Economics Experiment Station, Ames, IA. Project 2232.

[2]Graduate Research Associate and Professor, respectively. Department of Horticulture, Iowa State University. Ames, IA 50011.

ABSTRACT

Four laboratory experiments were conducted to determine the environmental conditions essential for ethephon-like growth regulation of Poa pratensis L. by ethylene and to test the assumption that ethephon predisposes Poa pratensis to ethylene sensitivity. Under 280 $\mu mol/m^2 sec$ irradiance, ethylene at 1000 $\mu L/L$ for eight days and ethephon at 1600 mg/L caused similar decreases in leaf and root growth and increases in tiller internode elongation. There was no response to ethylene, however, at any level from 27 to 3200 $\mu L/L$ if the treatment period was one day or if irradiance was 34 $\mu mol/m^2$ sec. Ethephon effects were constant in all environments tested except under 34 $\mu mol/m^2 sec$ for ten days in which it stimulated rather than inhibited leaf elongation. No synergistic effect could be found in applying ethylene sequentially to ethephon under high irradiance, although some additive effects were shown. Ethephon did not predispose Poa pratensis to ethylene sensitivity. An eight-day exposure period in a continuous air-exchange system under full sun conditions is recommended in obtaining complete sensitivity in Poa pratensis to exogenous ethylene.

Additional Index Words: growth regulation, controlled atmosphere, growth chamber, irradiance, partitioning, assimilates

INTRODUCTION

Plant hormones are a critical link between gene activity and morphological expression. Papers have been published describing hormone stimulation of gene activity (4, 10, 11, 18, 25, 27, 28, 33) from every hormone class, and recent advances in gene manipulation enable the development of new germplasm resulting in plant improvement. It is important, therefore, to develop methods of associating the presence or activity of a particular hormone with morphological traits.

In Poa pratensis (Kentucky bluegrass) ethephon inhibits leaf elongation while stimulating internodes to elongate in a normally compact stack of nodes (6, 39, 40, 45). This unique reaction of Poa pratensis to ethephon could serve as a tool in learning more about hormonal and genetic control of leaf and stem growth in perennial grasses. It is assumed that the growth-regulating activity of ethephon is due to its release of ethylene during catabolism in plant tissues. It is possible that the unusually high amount of ethylene interacts with other hormones in altering Poa pratensis morphogenesis. Several papers have been published in the study of hormone effects on leaf (2, 13, 19, 24, 32, 35, 39, 40, 41), stem (12, 32, 37, 39, 40, 41, 43), and coleoptile (14, 17, 19, 20, 30, 35, 42) growth in graminaeous species and of the interaction among the hormone classes in plant growth regulation (21, 31, 47). Specific associations of either ethephon or ethylene with other hormones in the growth of grasses have been noted (12, 17, 22, 24, 40). Once it is established that only ethylene from

ethephon catabolism triggers the morphogenic changes, correlations can be made with changes in endogenous cell constituents including the other hormone classes, mRNA, second messengers and enzymes.

There are four advantages in Poa pratensis that make it an ideal research tool. First, the growth of its leaves and stems is primarily one dimensional which simplifies the quantification of growth response. Coleoptile growth has been traditionally used for this purpose (26). Second, the partitioning of assimilates between the leaves and stems of a mature plant can be investigated, something that is impossible to address in coleoptile growth. Third, its structure allows exclusive treatment of its only exposed parts, the maturing leaves. The stem apex and crown are shielded by superposing leaves. Fourth, Poa pratensis can be easily cloned, thus eliminating genetic variance in replicated studies.

Poovaiah and Leopold (32) have shown pictorially that ethylene triggers a growth response qualitatively similar to that from ethephon treatment, but an attempt to verify their results revealed that ethephon effects were always evident while ethylene effects were sometimes absent. Ethephon apparently has a property that promotes greater ethylene efficacy. This may be due to its slow continual release of ethylene over a number of days, proximity to reaction sites, or predisposition of plant tissues to ethylene sensitivity by one of the other components in ethephon catabolism. The orthophosphate and chloride that are also produced in the reaction are usually considered by-products (46). Maynard and Swan (23) refer to 2-chloroethyl

phosphonic acid (ethephon) as one of the 2-chloroalkyl phosphonic acids which are phosphorylators of alcohol or phenol with the corresponding alk-1-ene (in this case, ethylene) and chloride ion as by-products. While in many cases, ethephon has been shown to cause plant responses characteristic of ethylene treatment, (5, 8, 32, 34, 44), it is important to recognize that either of the other products, especially phosphate, or the acidity of ethephon, itself, could contribute to the growth-regulating activity. Southwick et al. (36), for instance, found ethephon, phosphate, or chloride inhibited, whereas ethylene promoted seed germination or coleoptile growth in Oryza sativa L. and Echinochloa crus-galli L.

The purpose of this study was to determine the environmental conditions essential for ethephon-like growth regulation of Poa pratensis by ethylene and to test the assumption that ethephon predisposes Poa pratensis to ethylene sensitivity. Three objectives were addressed with the following experiments:

1 and 2. to compare the effects of ethephon at a rate recommended for Kentucky bluegrass turf with ethylene at an exposure duration and range of rates from a minimum that has proven to give positive results with other graminaeous species to a maximum equal in concentration to applied ethephon,

3. to compare, at a low irradiance level, ethephon effects with ethylene effects at a standard rate and a range of exposure durations within the time usually required for metabolism of ethephon,

4. to test, under full-sun conditions in the greenhouse, for a synergistic response in plants treated with either a low, medium, or high ethylene rate for eight days after ethephon treatment at half the recommended rate, compared to plants treated with ethephon or ethylene alone.

MATERIALS AND METHODS

Plant Culture

Propagules of a clone from 'Baron' Kentucky bluegrass were grown in potted soil in a greenhouse until they had at least one root 5 cm long. Older leaves from plants of uniform size were then stripped off leaving the two youngest exposed leaves. The plants were transferred to a hydroponic culture system having a nutrient solution modified from Pellett and Roberts (29) which is a Hoagland solution (15) modified for turfgrasses. This solution had, in mg/L, 100 potassium, 116 magnesium, 2 iron and 0.5 manganese compared to 63, 19, 1.2 and 0.25, respectively, in the Pellett and Roberts solution. All other elemental levels were identical. Each plant was held with Mortite (a pliable resin-based compound that can be found in most home-improvement stores; Mortell Co., P. O. Box 71, 550 N. Hobbie Ave., Kankakee, Ill. 60901) at the mouth of a flat-bottom 250-ml boiling flask double-wrapped with aluminum foil. The nutrient solution in the flasks was aerated from an air pump via 1.0-mm inside diameter (id) polyethylene tubing coming from a 2-cm id polyethylene manifold. The culture system was on a greenhouse bench with overhead supplemental irradiance from four LU1000-HPS (High Pressure Sodium) lamps in Sylvania Batwing Maxi-Gro luminaires (Sylvania Lighting Equipment, 21 Penn St, Fall River, MA 02724) supplying a PPFD (Photosynthetic Photon Flux Density) of 703 $\pm$ 16 $\mu mol/m^2$ sec. Plants were removed from the supplemental irradiance and aeration in complete blocks for treatment, then returned and allowed to grow until final data

were recorded. The solution of an entire block was replaced every 3 to 7 days during the growth periods before and after treatment, depending on the average size of the plants.

Treatment

Each block of plants with flasks was removed separately from the greenhouse bench and treated with ethephon and/or ethylene at the two- to three-leaf stage. The mortite sealed each plant immediately above the crown at the mouth of its flask thereby preventing adsorption of ethylene into the nutrient solution. The plants were treated in a continuous air-exchange roomette and gas-meting system according to Diesburg et al. (7).

Ethylene concentrations were chosen on the basis of two concepts. First, Ku et al. (20) and Suge (37) found that 10 μL/L ethylene caused maximal growth response in oat coleoptile and mesocotyl, respectively. Abeles (1) states that monocots, in general, are less sensitive to ethylene than dicots. In some plant growth systems ethylene at 1000 μL/L have been required to achieve maximal response (1). Second, ethephon was applied at 3200 mg/L. The highest possible concentration of ethylene evolved from ethephon at any given time would be 3200 μL/L. Ethylene concentration between 10 and 1000 μL/L was considered, therefore, to be the range most likely to cause a morphogenic change in Poa pratensis. Ethylene at 3000 or 3200 μL/L was applied to eliminate the possibility that applied concentrations would not be high enough.

Experiment One

Treatments were ethylene at 670 μL/L, ethephon at 3200 mg/L (the recommended rate for treatment of Poa pratensis turf), and a nontreated control exposed to identical roomette conditions for 12 hours. Additional ethephon-treated and nontreated controls were placed outside the roomettes. Laboratory conditions were 8.7 ± 0.9 $\mu mol/m^2$ sec PPFD and 23 ± 0.5 C.

Experiment Two

Treatments were ethylene at 27, 670, and 3200 μL/L, ethephon at 3200 mg/L and a nontreated control in roomettes for 24 hours. Laboratory conditions were 8.7 ± 0.9 $\mu mol/m^2$ sec PPFD and 23 ± 0.5 C.

Experiment Three

Treatments were ethylene at 100 μL/L for 1/2, 2, 5, and 10 days, 50% ethylene for 10 days, ethephon at 3200 mg/L for 10 days all in closed roomettes with stirring magnets, and nontreated controls both inside and outside a roomette. Laboratory conditions were 33.7 ± 4.4 $\mu mol/m^2$ sec PPFD and 27 ± 2 C.

Experiment Four

Treatments were ethephon at 1600 mg/L by itself inside and outside the roomettes, ethephon at 1600 mg/L plus ethylene at 10, 100, 1000, and 3000 μL/L, ethylene by itself at 1000 μL/L, a nontreated control all in roomettes for 8 days and a nontreated control outside the roomettes.

Greenhouse conditions were 280 $\pm$ 9 μmol/m^2sec PPFD and 23 $\pm$ 5 C.

Data

Measurements of plant growth in experiment 1 were taken as soon as differences were observed 12 to 14 days after treatment. In experiments 2 and 3, data were recorded when maximum response to treatment appeared to have occurred 23 to 27 days after treatment. Data in experiment 4 were recorded when plants had begun to recover from treatment effects, 30 to 33 days after the start of treatment. Growth of the entire plant was assessed by measuring individual and total lengths of leaves, rhizomes, rhizome internodes, and tiller internodes; counting the number of tillers, leaves, rhizomes, rhizome internodes, and tiller internodes; calculating average leaf number and length per tiller, rhizome, rhizome internode, and tiller internode length; recording the fresh or dry weights of tillers, rhizomes, and roots; and calculating total plant weight and tiller-rhizome-shoot/root weight ratios. Tiller weights were the sum of leaf and stem weights, while shoot weights were the sum of tiller and rhizomes weights.

RESULTS

Experiments One and Two

Neither ethephon nor ethylene affected total tiller number but ethephon increased total leaf number by 43% over nontreated plants. Ethephon and ethylene increased the average number of leaves per tiller by 33 and 10%, respectively (Tables 1, 3 and 4). Ethephon decreased average and total leaf lengths by 31 and 24%, respectively. Figures 1 and 3 show the average leaf lengths for each treatment in tillers 1 through 11 and 14, respectively. Ethylene had no effect on average leaf length in any of the tillers but showed a tendency toward effectiveness in experiment two at 27 and 3200 μL/L with tillers 8 through 13. Ethephon effectiveness was consistent across tillers.

Tiller one was the initial and only exposed tiller during treatment. Tiller two was growing at that time but was still small enough to be sealed by the Mortite (9, 38) from direct chemical or gas contact. Treatment-affected leaves four through seven in tiller one correspond to treatment-affected leaves one through four in tiller two (Figs. 2 and 4). Both sets of affected leaves were in their primordial stages of development during treatment.

Ethephon reduced root weight by 37% while stimulating 9 tiller internodes to elongate a total of 4.4 cm at an average of 0.5 cm per internode, compared to no elongated internodes in ethylene treated or nontreated plants (Tables 1, 2, 3 and 4). Ethylene at 3200 μL/L reduced root weight by 25% but did not stimulate internode elongation. Tiller

Table 1. Analyses of variance of Kentucky bluegrass response to ethephon ar

Source	df	Mean Square					
		Leaf					
		Total Num	Num in Tiller One	Num Per Tiller	Total Length	Average Length	Intern Num
Experiment One							
Treatments	4	91.9	2.1**	3.0**	15689**	29.9**	88.1**
670[a] vs Ethephon[b]	1	19.2	2.1*	3.7**	42225**	41.8**	235.2**
670 vs Control	1	218.7	0.5	0.5*	6328	0.2	104.5*
Ethephon vs Control	1	103.8	4.8**	7.1**	15861*	47.1**	26.1
Error	68	73.3	0.4	0.1	3578	1.6	16.6
Experiment Two							
Treatments	4	1600.2**	11.3*	3.4**	16629	27.8**	103.6
27 vs 670	1	757.5	6.7	0.1	15619	1.1	13.6
27 vs 3200	1	673.2	17.7*	0.1	1395	2.5	27.3
3200 vs Ethephon	1	2464.9**	2.0	9.1**	21991	57.6**	26.3
3200 vs Control	1	90.0	13.2*	0.1	31767	0.9	162.1
Error	92	356.7	4.6	0.1	29043	2.3	85.8
Experiment Four							
Treatments	8	232.1**	5.7**		4274*	20.5**	81.3
1000+[c] vs 1000	1	280.1**	9.4**		260	8.1**	242.0
1000+ vs Ethephon	1	5.6	2.0*		1232	2.4	10.9
1000 vs Ethephon	1	206.7*	2.7*		2623	1.7	144.5
1000 vs Control	1	60.5	1.4		3283	16.9**	1.4
10+ vs 100+	1	0.2	0		3542	2.1	12.5
100+ vs 3000+	1	2.0	0.9		6313	3.7*	29.4
10+ vs Ethephon	1	10.7	0.2		4219	5.4*	8.0
3000+ vs Ethephon	1	18.0	2.0*		7208*	7.7**	0.1
Error	70	33.4	0.4		1925	0.8	162.4

[a]Ethylene levels in μL/L.
[b]Ethephon applied at 3200 mg/L and control inside roomettes.
[c]+=in combination with ethephon at 1600 mg/L.
*, **Significant at the 0.05 and 0.01 probability levels, respectively.

of Kentucky bluegrass response to ethephon and ethylene

	Mean Squares									
		Leaf				Rhizome			Tiller	
al m	Num in Tiller One	Num Per Tiller	Total Length	Average Length	Intern Num	Total Intern Length	Average Intern Length	Intern Num	Total Intern Length	Average Intern Length
.9	2.1**	3.0**	15689**	29.9**	88.1**	195.3*	0.2	71.6**	13.7**	0.1
.2	2.1*	3.7**	42225**	41.8**	235.2**	454.2**	0.2	163.3**	30.1**	0.1
.7	0.5	0.5*	6328	0.2	104.5*	193.3*	0.2	0.1	0.1	0.1
.8	4.8**	7.1**	15861*	47.1**	26.1	66.5	0.1	154.1**	33.9**	0.1
.3	0.4	0.1	3578	1.6	16.6	55.7	0.2	4.1	2.9	0.1
.2**	11.3*	3.4**	16629	27.8**	103.6	181.7	0.2	636.2**	104.5**	0.2**
.5	6.7	0.1	15619	1.1	13.6	5.4	0.4*	0.2	0.1	0
.2	17.7*	0.1	1395	2.5	27.3	10.5	0.2	0.1	0.1	0
.9**	2.0	9.1**	21991	57.6**	26.3	32.2	0.1	942.6**	269.7**	0.2**
.0	13.2*	0.1	31767	0.9	162.1	308.5	0.2	0.1	0.1	0
.7	4.6	0.1	29043	2.3	85.8	159.8	0.1	16.9	6.8	0.1
.1**	5.7**		4274*	20.5**	81.3	186.0	0.6*	56.8**	220.1**	0.1*
.1**	9.4**		260	8.1**	242.0	595.4	0.1	27.7*	96.0*	0.1
.6	2.0*		1232	2.4	10.9	4.9	0.1	0.1	8.2	0
.7*	2.7*		2623	1.7	144.5	744.4	0.2	29.0*	48.1	0
.5	1.4		3283	16.9**	1.4	5.8	0.1	50.5**	130.7*	0.1
.2	0		3542	2.1	12.5	97.3	0.1	26.0*	150.0*	0.1
.0	0.9		6313	3.7*	29.4	112.3	0.1	7.7	8.2	0
.7	0.2		4219	5.4*	8.0	58.9	0.4	17.3*	16.7	0
.0	2.0*		7208*	7.7**	0.1	47.0	0.2	3.4	28.8	0.1
.4	0.4		1925	0.8	162.4	254.8	0.1	3.8	18.7	0.1

ng/L and control inside roomettes.
ephon at 1600 mg/L.
05 and 0.01 probability levels, respectively.

Table 2. Analyses of variance of Kentucky bluegrass weights in response to ethephon and ethylene, experiment two

Source	df	Dry Weight Mean Squares				
		Root	Tiller	Shoot	Shoot / Root	Tiller / Root
Trts.(Ethylene in μL/L)	4	0.020**	0.054	0.038	3.885**	3.168**
27 vs 670	1	<0.001	0.075	0.049	0.890	1.416
27 vs 3200	1	0.011	0.003	0.002	2.047	2.236*
3200 vs Ethephon	1	0.010	<0.001	0.007	5.102*	3.970*
3200 vs Control	1	0.027	0.107	0.053	0.791	0.397
Error	92	0.008	0.085	0.081	0.734	0.399

*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 3. Mean growth responses of Kentucky bluegrass to ethephon and ethylene treatment, experiment one

Response	Treatment					
	Ethylene 670 µL/L	Roomette Ethephon 3200 mg/L	Roomette Control	Outside Control	Outside Ethephon 3200 mg/L	LSD[a]
Leaf						
Number in Tiller One	7.5	8.0	7.2	7.2	7.9	0.5
Number per Tiller	3.3	4.0	3.0	3.0	3.8	0.3
Total Length (cm)	221.0	146.0	192.0	200.1	151.4	43.6
Average Length	7.9	5.6	8.1	8.3	5.5	0.9
Rhizome						
Internode Number	3.3	8.9	7.0	4.6	8.4	3.0
Total Intern. Lgth (cm)	7.5	16.5	13.4	9.7	16.3	5.9
Average Intern. Length	1.5	1.7	1.7	1.8	1.7	NS
Tiller						
Internode Number	0	5.0	0	0	3.3	1.5
Total Internode Length	0	3.5	0	0	2.3	1.8
Average Intern. Length	0	0.6	0	0	0.5	0.3
Fresh Root Weight (g)	3.71	2.22	3.39	3.78	2.43	0.89

[a]Significant at the 0.05 probability level.

Table 4. Mean growth responses of Kentucky bluegrass to treatment with ethephon and ethylene, experiment two

Response	Treatment					
	Ethylene 27 µL/L	Ethylene 670 µL/L	Ethylene 3200 µL/L	Ethephon 3200 mg/L	Control	LSD[a]
Leaf						
Total Number	39.6	47.2	47.2	63.0	44.2	1.9
Number in Tiller One	7.3	8.2	8.7	9.1	7.5	1.3
Number per Tiller	3.6	3.6	3.5	4.5	3.5	0.2
Average Length (cm)	11.7	11.4	11.2	8.8	11.6	1.0
Rhizome						
Intern Number	11.1	9.6	8.8	10.6	4.9	6.0
Total Intern Lgth (cm)	12.5	13.0	10.8	12.7	5.4	8.2
Average Intern Length	1.0	1.3	1.2	1.1	1.0	0.2
Tiller						
Intern Number	0	0	0	13.0	0	2.7
Total Intern Length	0	0	0	5.3	0	1.7
Average Intern Length	0	0	0	0.4	0	0.3
Weights (g)						
Fresh Root	2.89	2.80	2.54	1.95	3.00	0.71
Fresh Tiller	2.57	2.68	2.41	2.37	2.73	NS
Dry Tiller	0.78	0.86	0.76	0.77	0.89	NS
Fresh Shoot	3.17	3.15	2.93	2.73	3.07	NS
Weight Ratios						
Fresh Shoot/Root	1.12	1.14	1.18	1.61	1.13	0.25
Dry Shoot/Root	3.26	3.65	3.85	4.64	3.52	0.63
Fresh Tiller/Root	0.90	0.96	0.97	1.36	0.94	0.15
Dry Tiller/Root	2.81	3.27	3.39	4.10	3.15	0.47

[a]Significant at the 0.05 probability level.

Figure 1. Average tiller leaf lengths in response to ethephon treatment and a 12-hour exposure to ethylene, experiment one

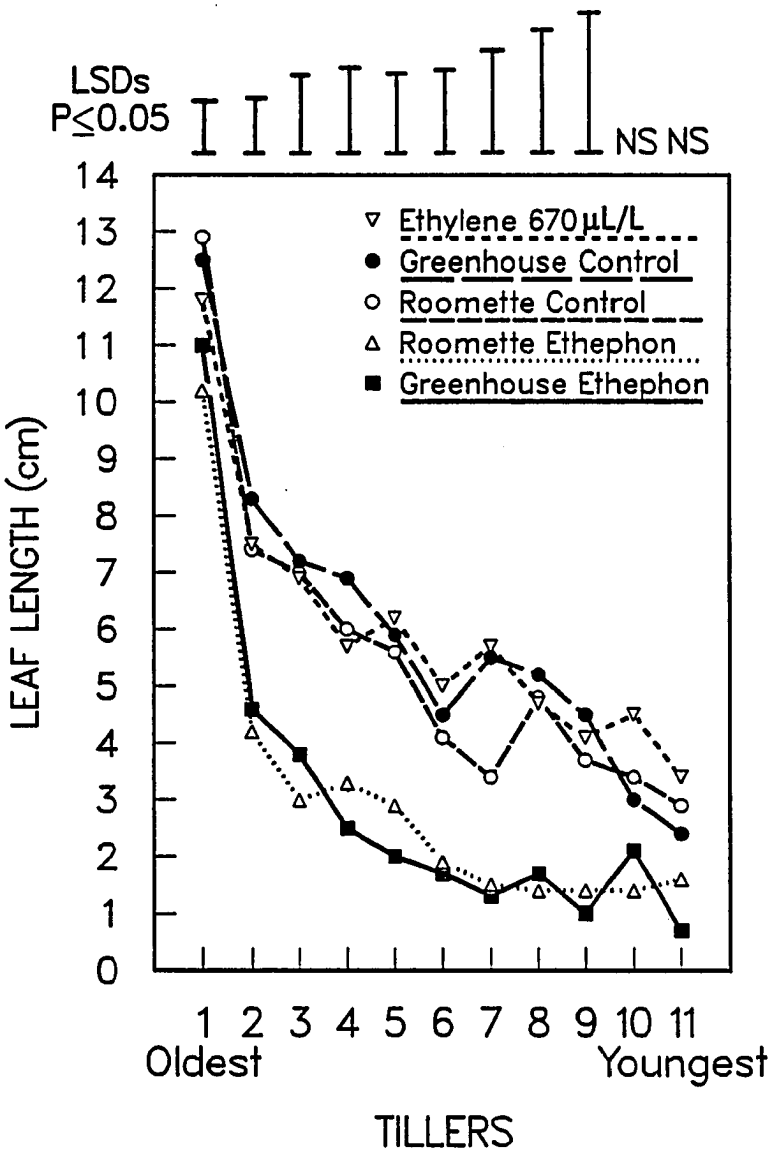

LSDs
P≤0.05
NS NS
Ethylene 670µL/L
Greenhouse Control
Roomette Control
Roomette Ethephon
Greenhouse Ethephon
LEAF LENGTH (cm)
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
1 2 3 4 5 6 7 8 9 10 11
Oldest
Youngest
TILLERS

Figure 2. Individual leaf lengths of the two oldest tillers in response to ethephon treatment and a 12-hour exposure to ethylene, experiment one

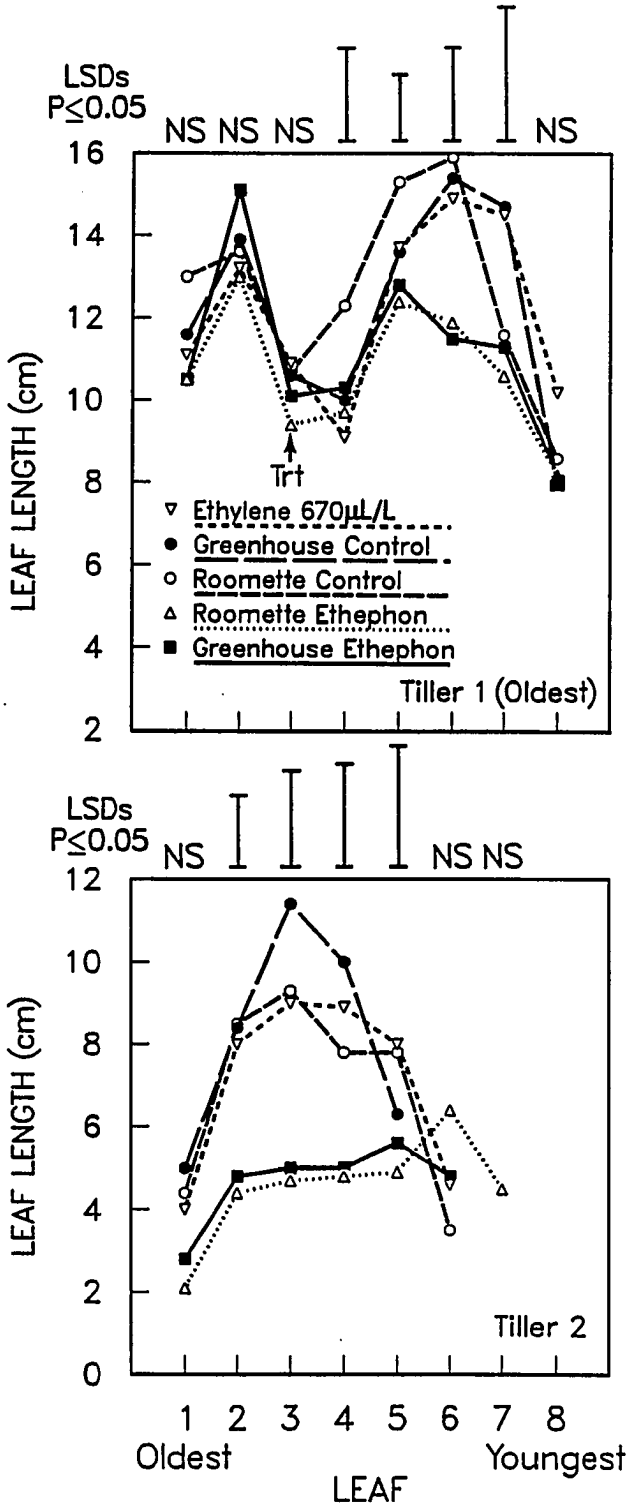

LSDs
P≤0.05
NS NS NS NS
LEAF LENGTH (cm)
16
14
12
10
8
6
4
2
Trt
Ethylene 670µL/L
Greenhouse Control
Roomette Control
Roomette Ethephon
Greenhouse Ethephon
Tiller 1 (Oldest)
LSDs
P≤0.05
NS NS NS
LEAF LENGTH (cm)
12
10
8
6
4
2
0
Tiller 2
1 2 3 4 5 6 7 8
Oldest
Youngest
LEAF

Figure 3. Average tiller leaf lengths in response to ethephon treatment and a 24-hour exposure to ethylene, experiment two

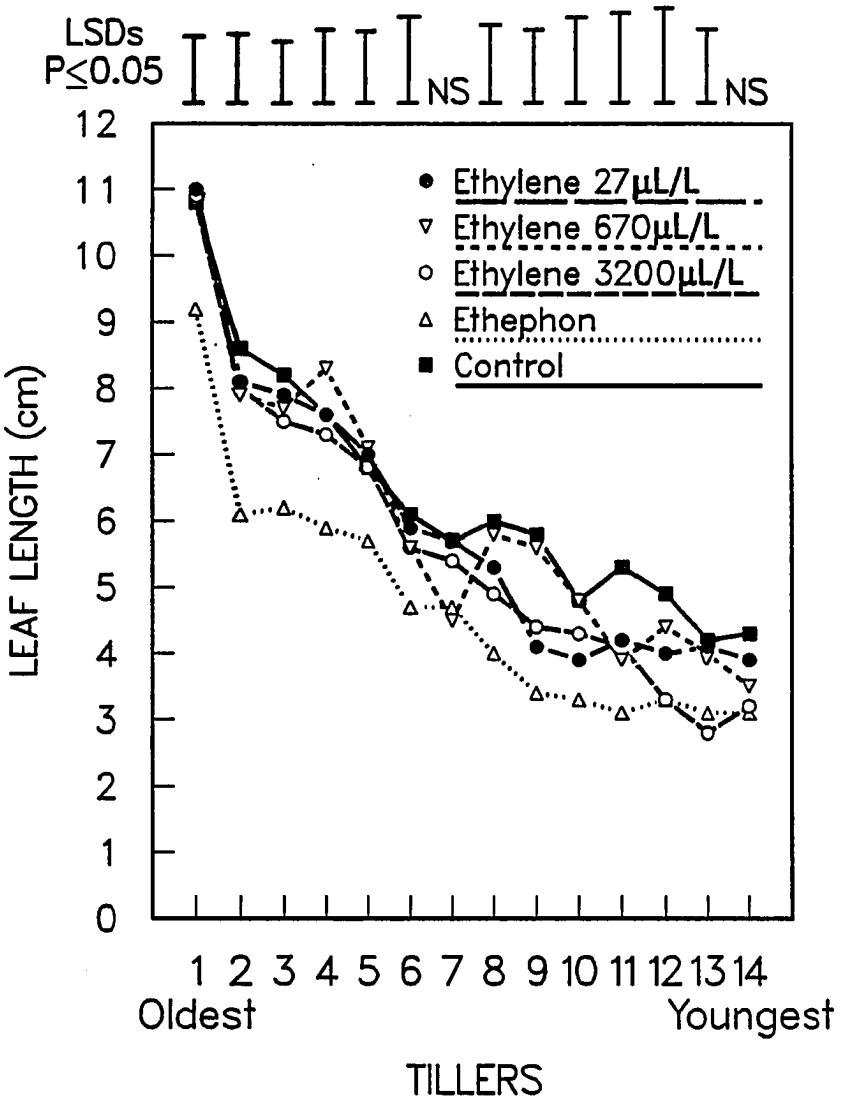

LSDs
P≤0.05
NS
NS
Ethylene 27µL/L
Ethylene 670µL/L
Ethylene 3200µL/L
Ethephon
Control
LEAF LENGTH (cm)
0
1
2
3
4
5
6
7
8
9
10
11
12
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Oldest
Youngest
TILLERS

Figure 4. Individual leaf lengths of the two oldest tillers in response to ethephon treatment and a 24-hour exposure to ethylene, experiment two

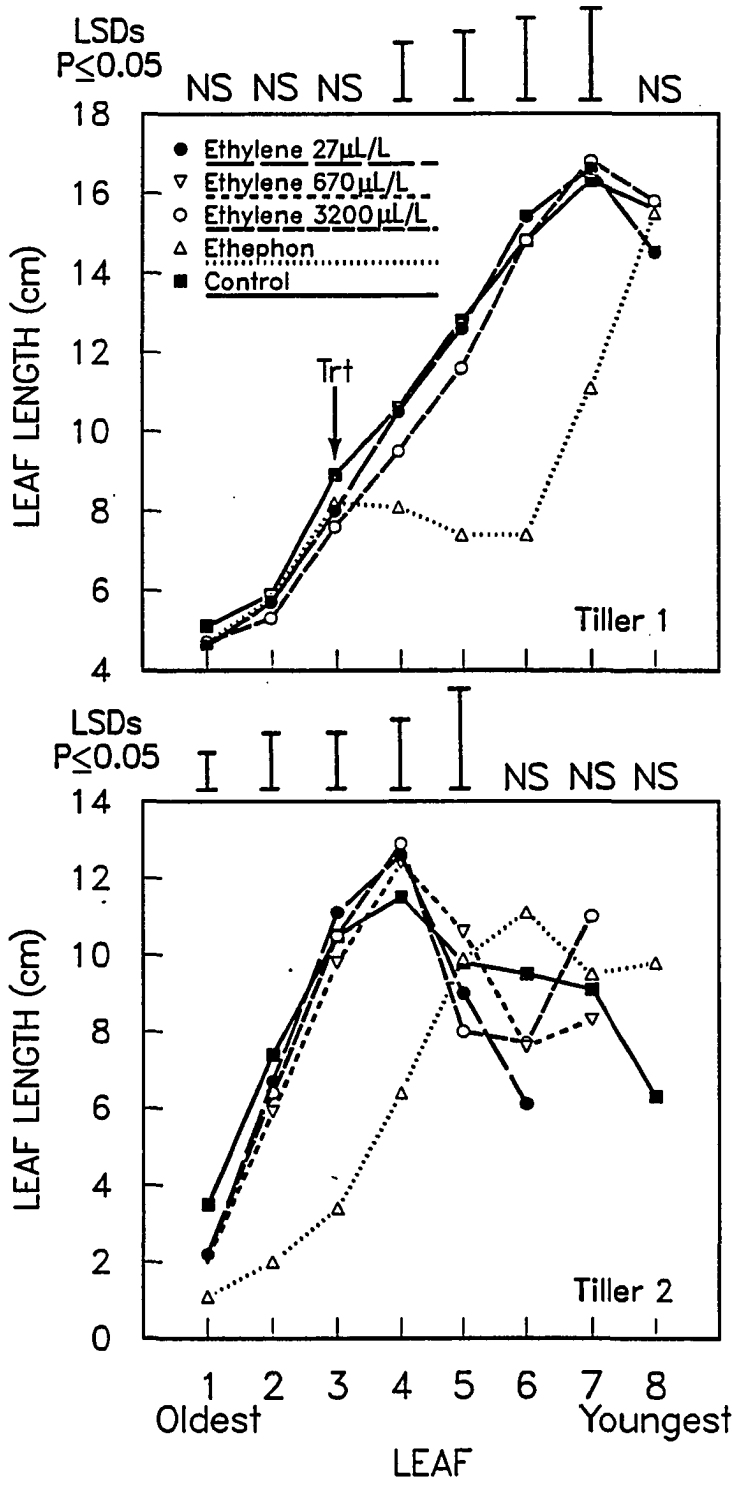

LSDs
P≤0.05
NS NS NS
NS
Ethylene 27µL/L
Ethylene 670µL/L
Ethylene 3200µL/L
Ethephon
Control
Trt
Tiller 1
LEAF LENGTH (cm)
18
16
14
12
10
8
6
4
LSDs
P≤0.05
NS NS NS
Tiller 2
LEAF LENGTH (cm)
14
12
10
8
6
4
2
0
1 2 3 4 5 6 7 8
Oldest
Youngest
LEAF

Table 5. Intertrait correlations computed from obervations over all treatments, experiment two

	Tiller Number	Leaf Number	Dry Tiller Weight	Dry Rhizome Weight	Dry Root Weight
Tiller Internode Number	0.23*	0.75**	-0.10	-0.17	-0.28*
Tiller Internode Length	0.23*	0.68**	-0.07	-0.18	-0.28*
Rhizome Number	-0.37**	-0.12	-0.33**	0.94**	-0.19
Rhizome Length	-0.29**	-0.14	-0.23*	0.94**	-0.08
Rhizome Internode Number	-0.31**	0.02	-0.29*	0.90**	-0.20
Rhizome Internode Length	-0.33**	-0.01	-0.30**	0.90**	-0.21
Fresh Tiller Weight	0.78**	0.40**	0.97**	-0.03	0.89**
Fresh Rhizome Weight	-0.18	-0.04	-0.11	0.97**	0.04
Fresh Root Weight	0.55**	0.06	0.73**	0.10	0.91**

* and ** Significant at the 0.05 and 0.01 levels, respectively.

and shoot weights were not affected by any treatment. As a result of the lower root weights from ethephon treatment, shoot/root and tiller/root dry weight ratios were 32 and 30% higher than those of nontreated plants, respectively.

Rhizome growth was highly variable within and between treatments and between experiments. No consistent effects could be obtained.

Intertrait correlations in Table 5 reveal that the ethephon-treated plants, having greater tiller internode number and length, also had a greater number of tillers and total leaf number with less root weight. Tiller internode number and length were not, however, associated with tiller or rhizome weights. Conversely, plants with greater rhizome number, length, internode number and internode length had a lower number of tillers and tiller weight, higher rhizome weight, and no association with root weight. Fresh weights of roots, tillers and rhizomes were highly correlated with their dry weights.

Experiment Three

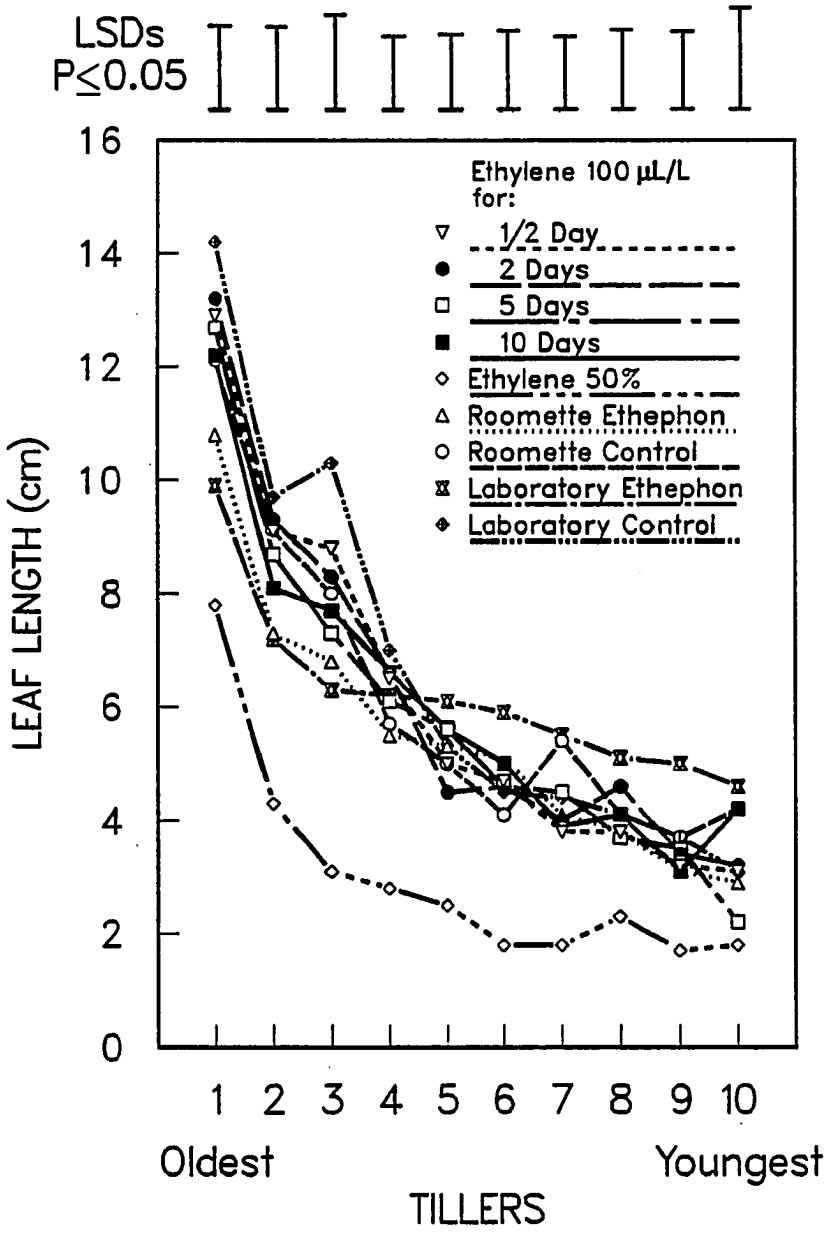
Carbon dioxide concentration inside the closed roomettes changed from 640 μL/L pretreatment to 1143 μL/L 18 hours after treatment initiation to 368 μL/L on the tenth day of treatment. Oxygen concentration dropped from 12.2 to 11.9% while ethylene concentration raised to 2.2 and 10.3 μL/L in roomettes with no treatment and ethephon treatment, respectively.

Table 6 and Figure 5 show the results of treatment with 100 μL/L ethylene for different time durations from half to ten days compared to

Table 6. Mean growth responses of Kentucky bluegrass to ethephon and ethylene treatment, experiment three

	Treatment									
		Ethylene 100 µL/L								
Response	50% Ethylene	1/2 Day	2 Day	5 Day	10 Day	Roomette Control	Roomette Ethephon	Outside Control	Outside Ethephon	LSD
Rhizome										
Number	2.2	2.3	1.2	3.6	4.4	3.8	1.7	1.8	3.8	2.5
Total Length	23.1	20.1	24.9	18.7	36.1	21.7	8.8	10.6	61.8	26.1
Internode Number	2.4	0	0	0	0.6	1.6	0.1	0	9.8	4.7
Tiller										
Internode Number	21.8	0.6	0.8	0.7	1.4	0.7	7.0	0.3	27.1	5.0
Internode Length	13.2	0.3	1.1	0.6	1.0	1.0	4.4	0.6	12.6	3.3
Fresh Weights										
Root	0.35	1.07	0.88	0.84	0.80	0.76	0.56	1.04	0.98	0.28
Rhizome	0.07	0.12	0.06	0.11	0.17	0.17	0.04	0.07	0.28	0.16
Leaf	1.35	2.21	2.19	2.02	1.84	1.84	1.99	2.58	3.30	0.53
Plant	1.77	3.41	3.13	2.98	2.81	2.77	2.59	3.69	4.57	0.77
Shoot/Root Ratio	4.31	2.13	2.56	2.44	2.30	2.50	3.62	2.60	4.01	0.78

Figure 5. Average tiller leaf lengths in response to treatment with ethephon, 50% ethylene for ten days, and 100 μL/L ethylene over a range of exposure periods, experiment three


LSDs
P≤0.05
LEAF LENGTH (cm)
16
14
12
10
8
6
4
2
0
Ethylene 100 µL/L
for:
1/2 Day
2 Days
5 Days
10 Days
Ethylene 50%
Roomette Ethephon
Roomette Control
Laboratory Ethephon
Laboratory Control
1 2 3 4 5 6 7 8 9 10
Oldest
Youngest
TILLERS

no treatment and exposure to 50% ethylene for ten days. The 50% ethylene was the only treatment to reduce leaf elongation (55%). Ethephon treatment outside the roomettes caused 30% longer average leaf lengths than those of nontreated plants outside the roomettes in tillers five through ten. Ethephon and ethylene stimulated 7.0 and 21.8 tiller internodes to elongate a total of 4.4 and 13.2 cm while reducing root fresh weight by 26 and 54%, respectively. Ethephon treatment outside the roomettes caused internode elongation similar to that of the 50% ethylene treatment, but it increased root weight 42%. The 50% ethylene treatment increased shoot/root fresh weight ratio 72% over the control.

Experiment Four

Plants grown for 33 days after the start of treatment had enough time for development of axillary tillers at extended nodes. Treatment with ethephon and ethylene by itself stimulated the growth of axillary tillers 29 and 21% over the control in tiller one as well as 50 and 30% more in tiller two, respectively. Ethylene added to ethephon had no additional effect. Ethephon treatment increased total, tiller one and tiller two leaf number 36, 18 and 52%, respectively, over the roomette control (Tables 1 and 8). Ethylene applied sequentially at 10 and 100 μL/L to ethephon had no additional effect, but at 1000 and 3000 μL/L ethylene plus ethephon increased leaf number further in tiller one by 28% over the control.

Ethephon plus 3000 μL/L ethylene was the only effective treatment on total leaf length which it decreased to 16% less than the roomette

Table 7. Analyses of variance of Kentucky bluegrass weights in response to ethephon and ethylene, experiment four

Source	df	Mean Squares							
			Weight						
		Axillary Tiller Number	Fresh Shoot	Fresh Leaf	Dry Leaf	Fresh Root	Dry Stem	Dry Stem / Leaf	Fresh Shoot / Root
Trts.(Ethylene in µL/L)	8	3.8**	0.654*	0.440**	0.017	1.457**	0.010**	0.104**	0.287
1000+[a] vs 1000	1	0.2	0.064	0.029	<0.001	0.100	0.002	0.037	0.173
1000+ vs Ethephon	1	1.4	0.328	0.121	0.011	0.155	0.001	0.001	0.031
1000 vs Ethephon	1	2.7	0.103	0.269	0.012	0.006	0.005	0.044	0.095
1000 vs Control	1	6.7**	1.389*	0.748**	0.043	0.580	0.012**	1.201**	0.003
10+ vs 100+	1	0.5	0.014	0.170	0.019	0.047	<0.001	0.141	0.007
100+ vs 3000+	1	1.4	0.294	0.347	0.016	0.118	0.001	0.468*	0.007
10+ vs Ethephon	1	0.9	0.236	0.284	0.019	0.140	<0.001	0.013	0.063
3000+ vs Ethephon	1	0.2	0.828	0.503*	0.016	0.252	0.001	0.071	0.236
Error	80	1.0	0.446	0.104	0.016	0.352	0.002	0.047	0.253

[a]In combination with ethephon at 1600 mg/L.
*, ** Significant at the 0.05 and 0.01 probability levels, respectively.

Table 8. Mean growth responses of Kentucky bluegrass to treatment with ethephon and ethylene, experiment four

Response	Treatment							
	Ethephon[a] plus Ethylene µL/L							
	10	100	1000	3000	Con	Ethephon 1600mg/L	Ethylene 1000 µL/L	LSD[b]
Leaf								
Total Num	40.8	40.6	40.3	41.2	28.8	39.2	32.4	5.4
Num in Til One	8.7	8.7	9.1	9.1	7.1	8.4	7.7	0.6
Num in Til Two	6.6	6.4	5.9	6.6	4.2	6.4	5.1	0.7
Total Leaf Lgth	236.4	264.5	250.5	227.0	269.9	267.1	242.9	41.2
Avg Leaf Lgth	5.8	6.5	6.2	5.6	9.5	6.9	7.5	0.9
Avg Rhizome Intern Lgth	1.4	1.1	1.1	1.3	1.4	0.9	1.3	0.4
Tiller								
Intern Num	12.0	22.0	17.7	19.7	0.3	15.3	9.7	7.5
Total Intern Lgth	6.9	11.1	10.2	8.8	0.1	10.3	5.9	3.4
Avg Intern Lgth	0.6	0.5	0.6	0.5	0.1	0.7	0.7	0.4
Axillary Num	6.7	6.4	6.8	6.3	5.2	6.7	6.3	0.7
Weights								
Fresh Root	1.56	1.66	1.55	1.50	2.06	1.74	1.70	0.56
Fresh Leaf	1.19	1.39	1.28	1.11	1.61	1.44	1.20	0.30
Dry Leaf	0.39	0.45	0.40	0.39	0.50	0.45	0.40	0.12
Dry Stem	0.16	0.16	0.15	0.17	0.08	0.16	0.13	0.04
Fresh Shoot	2.06	2.12	2.02	1.86	2.69	2.29	2.14	0.63
Ratios								
Dry Stem/Leaf	0.43	0.37	0.37	0.48	0.15	0.37	0.34	0.11
Fresh Shoot/Root	1.48	1.38	1.52	1.37	1.30	1.60	1.32	0.47

[a]Ethephon at 1600 mg/L.
[b]Significant at the 0.05 probability level.

control. Ethylene, ethephon, and ethephon plus 10 or 3000 μL/L ethylene caused progressively shorter average leaf lengths at 21, 27, 40% less than the roomette control, respectively. Figure 6 shows the comparison among treatments of average leaf lengths for each set of tillers one through six in two groups. The first tiller of the first group is the originally propagated 'mother' shoot while tillers two through six developed intravaginally from lateral buds. The first tiller of the second group was an early extravaginal tiller from the mother shoot which grew rhizomatously for a short distance, then emerged through the Mortite and developed its own set of intravaginal tillers two through six. This growth sequence occurred consistently in all experimental units. Ethephon plus 3000 μL/L ethylene consistently yielded among the lowest numbers in average leaf length in the first group, although its effects were not different from those of ethephon alone or in combination with the other ethylene levels. Likewise, ethephon plus 10 μL/L ethylene yielded values consistently among the lowest in the second group. Ethylene alone at 1000 μL/L actually stimulated leaf elongation in tillers three through six of the first group. Average leaf lengths in tillers four and five were 29 and 60% greater than those of the control, respectively. Similar growth stimulation did not occur in the second tiller group. Figure 7 is a comparison of individual leaf lengths in the fourth tiller of each group. Length differences in tiller four of the first group occurred in the more recently developed leaves and not the oldest ones.

A comparison of individual leaf lengths in the first tiller of each

Figure 6. Average tiller leaf lengths in response to an eight-day treatment with ethephon, 1000 μL/L ethylene, and ethylene at three levels applied sequentially to ethephon, experiment four. [a]+=ethylene applied during ethephon degradation

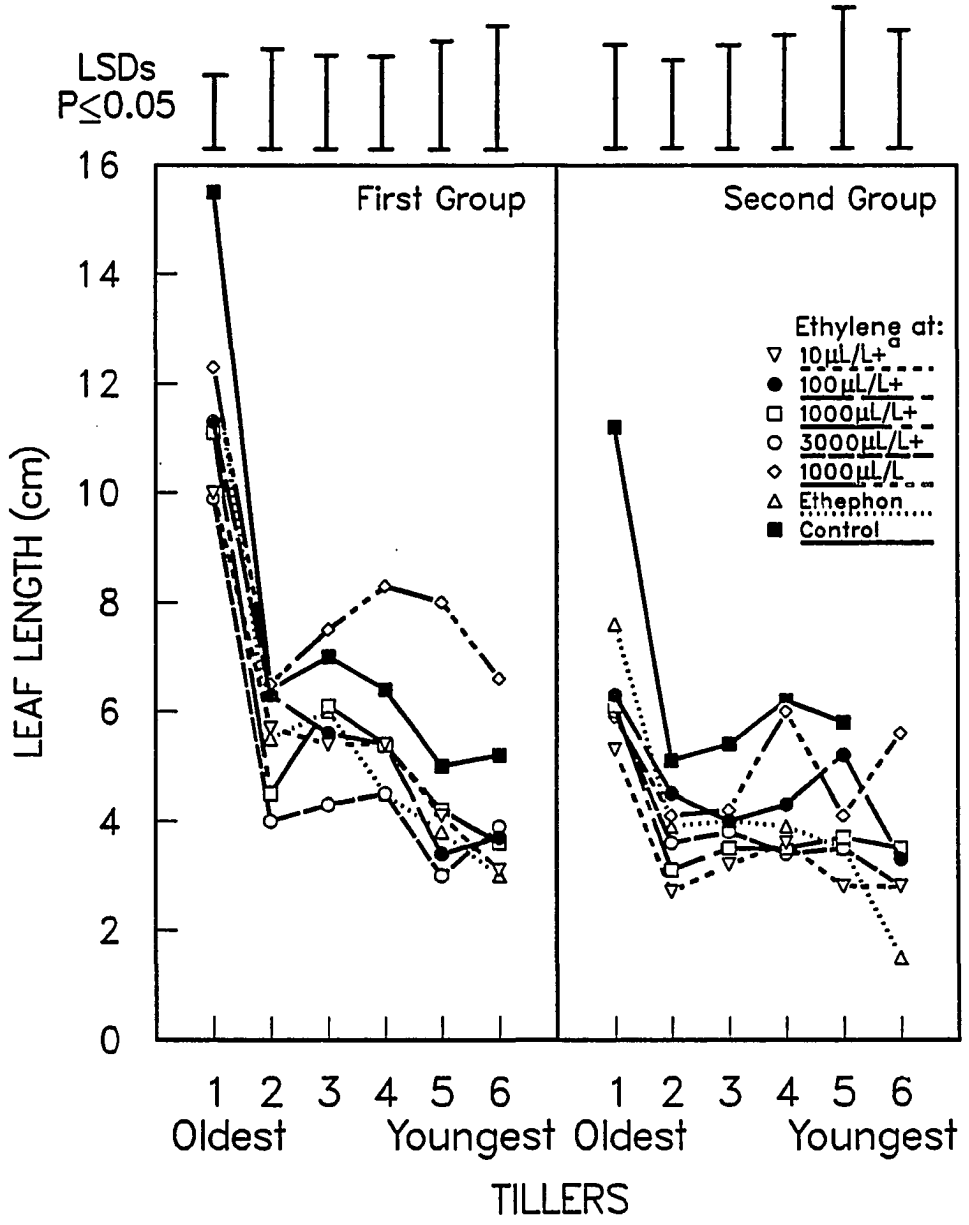
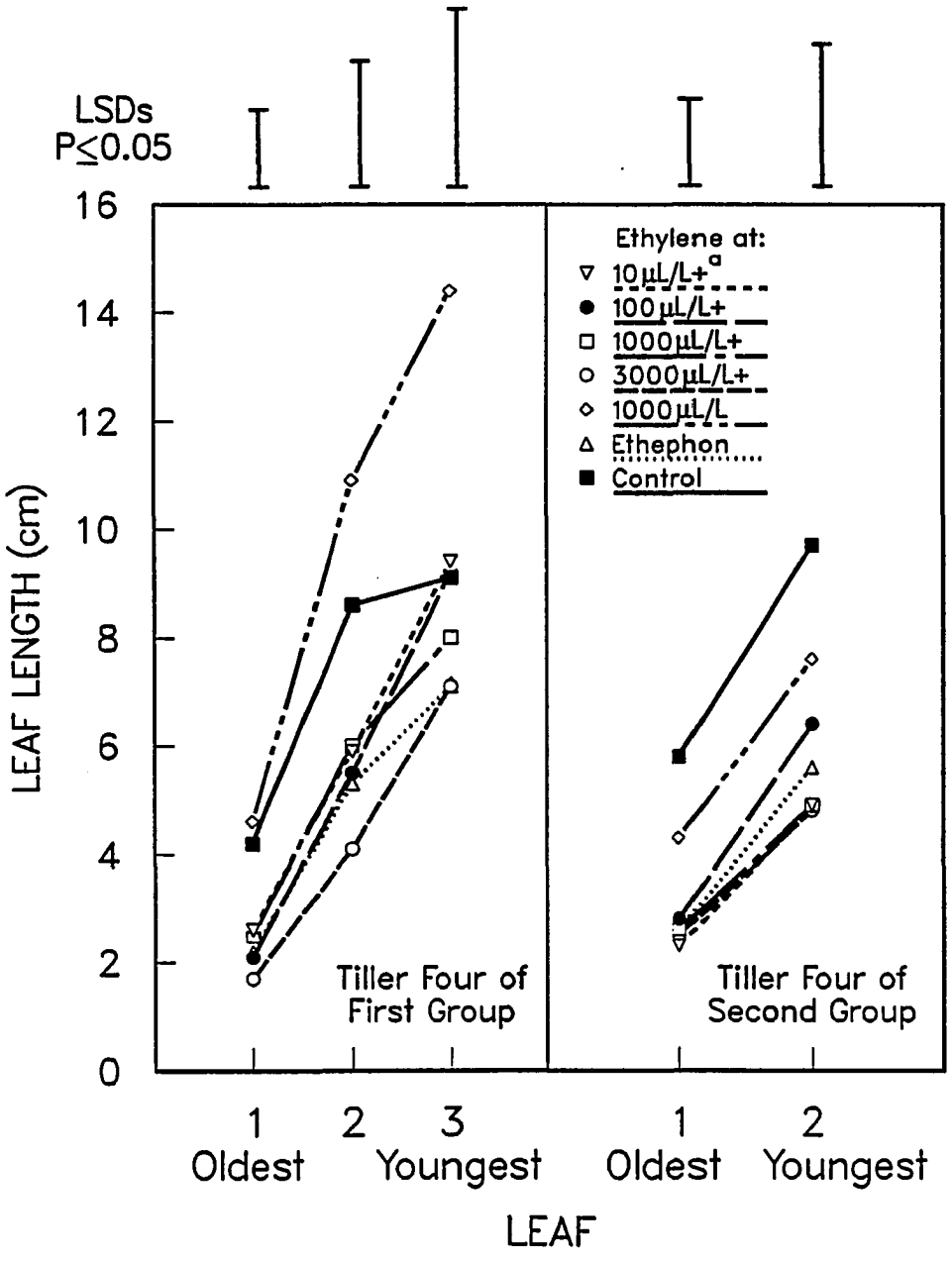

LSDs
P≤0.05
First Group
Second Group
Ethylene at:
10µL/L+
100µL/L+
1000µL/L+
3000µL/L+
1000µL/L
Ethephon
Control
LEAF LENGTH (cm)
0
2
4
6
8
10
12
14
16
1 2 3 4 5 6
Oldest
Youngest
1 2 3 4 5 6
Oldest
Youngest
TILLERS

Figure 7. Individual leaf lengths of two fourth tillers, each from a tiller group in experiment four, in response to an eight-day treatment with ethephon, 1000 μL/L ethylene, and ethylene at three levels applied sequentially to ethephon. [a]+=ethylene applied during ethephon degradation


LSDs
P≤0.05
LEAF LENGTH (cm)
16
14
12
10
8
6
4
2
0
Ethylene at:
10µL/L+a
100µL/L+
1000µL/L+
3000µL/L+
1000µL/L
Ethephon
Control
Tiller Four of
First Group
Tiller Four of
Second Group
1
2
3
Oldest
Youngest
1
2
Oldest
Youngest
LEAF

group is shown in Figures 8 and 9. As in the first two experiments, leaves four through seven in tiller one of the first group correspond to leaves one through four in tiller one of the second group. Ethylene alone at 1000 μL/L was as effective as ethephon plus ethylene at all levels except 3000 μL/L. Ethephon plus 10 μL/L ethylene consistently yielded among the lowest values in tiller one of the second group. The effects of ethylene alone at 1000 μL/L diminished more rapidly than those of any other treatment, and were absent during growth of the seventh and eighth leaves. All additions of ethylene to ethephon were more effective than ethephon alone in tiller one of the first group, and nearly so in tiller one of the second group, but they were not different from one another.

Tiller internode number and total length were stimulated by all treatments to different extents (Tables 7 and 8). Ethephon plus 100 μL/L ethylene caused greatest tiller internode number at 22.0 and elongation to 11.1 cm, while ethephon plus 1000 and 3000 μL/L ethylene and ethephon alone were not different from one another averaging 17.6 tiller internodes with total elongation to 9.8 cm. Weakest stimulation came from ethephon plus 10 μL/L ethylene and 1000 μL/L ethylene alone with tiller internode numbers averaging 10.8 and total elongation to 6.4 cm. Average tiller internode lengths were similar among all treatments at 0.6 cm.

Rhizome growth was highly variable within treatments. It appears that all ethephon treatments with or without ethylene, reduced rhizome number and total length and rhizome internode number and total length,

Figure 8. Individual leaf lengths of the oldest tiller in group one in response to an eight-day treatment with ethephon, 1000 μL/L ethylene, and ethylene at three[a] levels applied sequentially to ethephon, experiment four. [a]+=ethylene applied during ethephon degradation

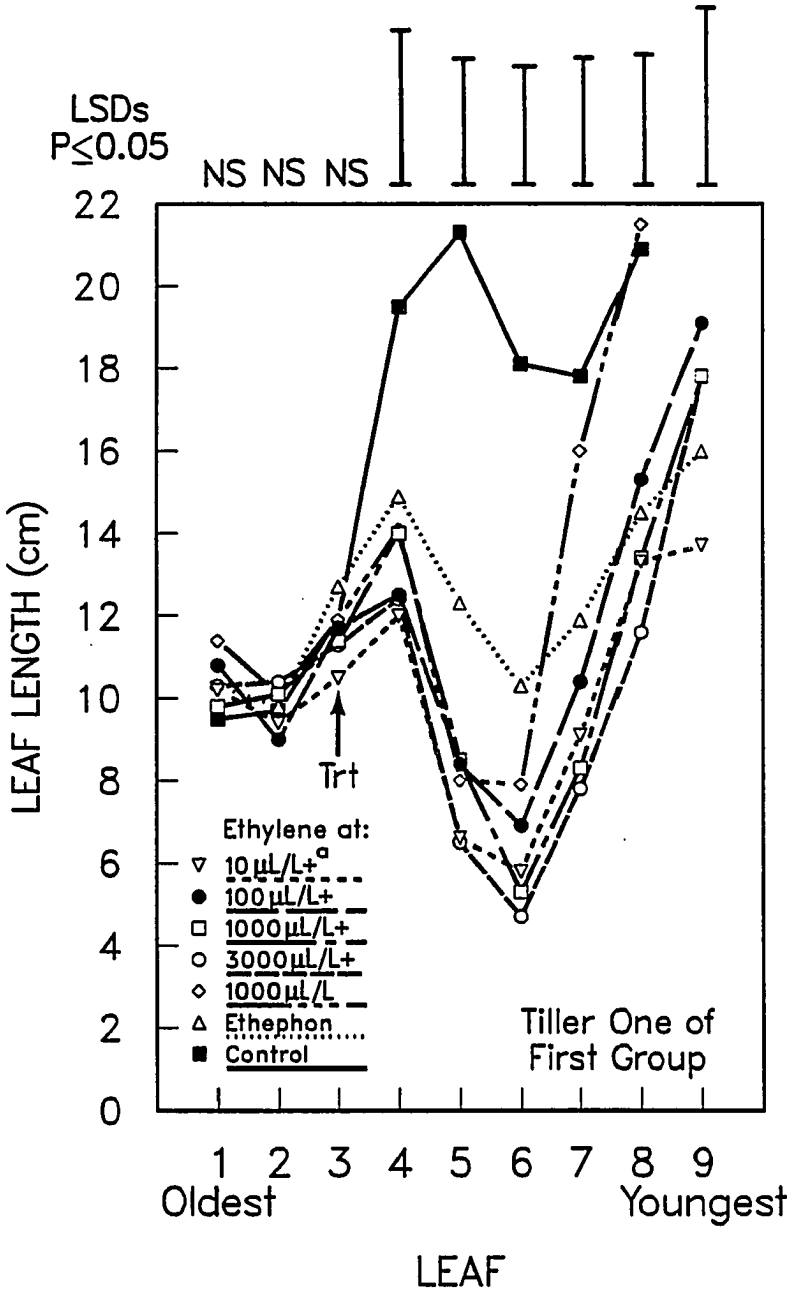
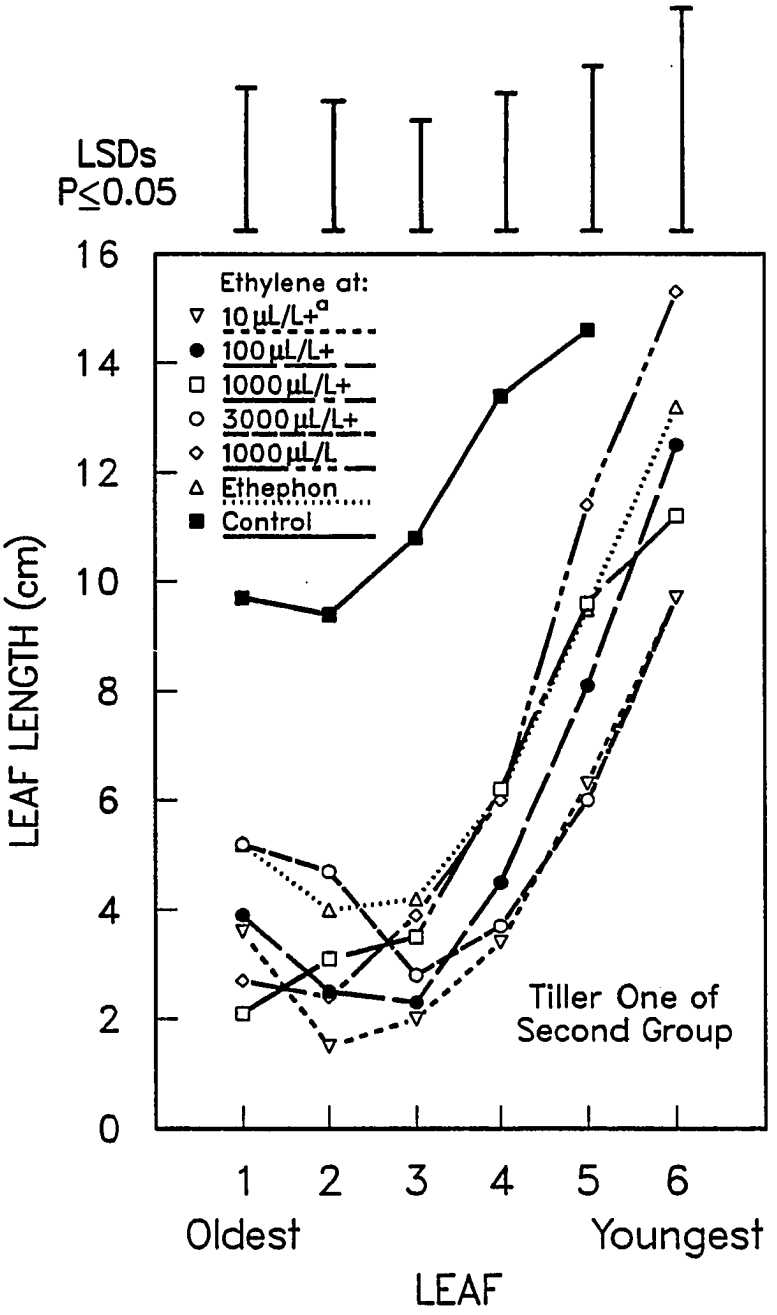

LSDs
P≤0.05
NS NS NS
LEAF LENGTH (cm)
22
20
18
16
14
12
10
8
6
4
2
0
Trt
Ethylene at:
10 µL/L+a
100 µL/L+
1000 µL/L+
3000 µL/L+
1000 µL/L
Ethephon
Control
Tiller One of
First Group
1 2 3 4 5 6 7 8 9
Oldest
Youngest
LEAF

Figure 9. Individual leaf lengths of the oldest tiller in group two in response to an eight-day treatment with ethephon, 1000 µL/L ethylene, and ethylene at three levels applied sequentially to ethephon, experiment four. [a]+=ethylene applied during ethephon degradation


LSDs
P≤0.05
16
14
12
10
8
6
4
2
0
LEAF LENGTH (cm)
Ethylene at:
10 µL/L+a
100 µL/L+
1000 µL/L+
3000 µL/L+
1000 µL/L
Ethephon
Control
Tiller One of
Second Group
1
2
3
4
5
6
Oldest
Youngest
LEAF

even though statistical tests were not significant. Ethephon treatment alone definitely reduced average rhizome internode length by 36%, while treatment with any ethylene level sequential to ethephon removed that effect.

Ethephon and ethylene alone and together decreased root fresh weight to 22% less than the control while ethylene alone and ethephon alone or with ethylene increased stem dry weights 62 and 100%, respectively. Leaf fresh weights were reduced similarly by ethylene and all ethephon plus ethylene treatments by an average of 23% while ethephon alone had little effect. Tiller and rhizome fresh and dry weights as well as rhizome/root fresh weight ratios were not affected by any treatments. Shoot fresh weights were reduced, however, by ethylene and/or ethephon treatments. Ethephon alone was the least effective while 3000 μL/L ethylene plus ethephon was the most effective at 15 and 31%, respectively. As a result of these relative changes, stem/leaf dry weight ratios were increased by all treatments of ethephon and/or ethylene but the greatest increase occurred with ethephon plus 10 or 3000 μL/L ethylene at 203% greater than that of the control, compared to 142% greater from the other treatments. Shoot/root ratios, however, were not changed with any treatment, because both shoot and root fresh weights were similarly reduced.

DISCUSSION

The results of experiments one and two show that Poa pratensis is not visibly responsive to a one-day exposure to ethylene at any concentration from 27 to 3200 μL/L. This supports the statement by Abeles (1) that growth regulation by ethylene in vegetative tissues occurs only as long as ethylene is present. Ethylene does not trigger a chain of biochemical events that can proceed on their own in the absence of ethylene. One important property of ethephon, therefore, is that it releases ethylene over a long period of time, probably four to ten days depending on temperature and pH (3).

The intertrait correlations in Table 5 reveal an important aspect in the partitioning of assimilates in Poa pratensis growth. Increase in stem size occurred at the expense of root weight and not rhizome weight. Conversely, increase in rhizome size occurred at the expense of tiller weight and not root weight. Energy flow in the form of carbohydrates seems to go from roots to tillers to rhizomes.

The experiments demonstrate an irradiance requirement for sensitivity to both ethephon and ethylene. Since all ethylene concentrations caused a growth response in experiment four, the 100 μL/L ethylene treatment in experiment three also should have been effective, but it was not. Most evidence from other research indicates that the effects of light on plant sensitivity to ethylene are mediated through CO_2 concentration (16). Carbon dioxide seems to be acting as a competitive inhibitor to ethylene at ethylene binding sites. The low

irradiance level of experiments one, two and three, therefore, could have decreased plant sensitivity to applied ethylene indirectly due to the build up of high internal CO_2 levels caused by reduced photosynthetic and carbon fixation rates. Conversely, the high irradiance level in experiment four could have maintained high photosynthetic and carbon fixation rates causing low internal CO_2 levels, thus allowing plant sensitivity to applied ethylene.

It is not likely that carbon dioxide deficiency was slowing plant metabolism and causing plant insensitivity to ethylene. Carbon dioxide concentrations in the roomettes remained above 300 μL/L while air turbulence from the stirring magnets limited localized CO_2 deficiency near the leaf surfaces. Additionally, ethephon was equally ineffective in reducing leaf lengths of plants both inside and outside the closed roomettes. The strong response to 50% ethylene in the closed roomettes indicates that the plants were capable of responding, even though they were in a suboptimal growth environment.

Leaf elongation was actually increased by ethephon in the low irradiance experiment when applied to plants outside the roomettes. This abnormality, as well as the lack of response to 100 μL/L ethylene, appears to be associated with root weight. The 50% ethylene, which caused short leaves in experiment three, lowered root weights 46% in that experiment while root weights of plants treated with the 100 μL/L ethylene were not affected. In corollary the root weights of the ethephon-treated plants outside the roomettes in experiment three were higher than those of the nontreated plants outside the roomettes.

Ethephon usually decreases root weights while decreasing leaf lengths. Van Andel (40) found that leaves of ethephon-treated plants were short because of reduced cell division and not because of reduced cell elongation. Individual leaf measurements in experiment four reveal that shortness occurred in leaves that grew to maturity after the exposure to ethylene. The affected leaves were probably in their primordial stage of growth at that time. Mitosis, which is very active during that stage, was probably inhibited resulting in fewer cells to expand and differentiate into leaves. Investigation should be directed toward finding a factor or substance associated in common with reduced root volume or activity, and reduced cell division in the leaves.

The stimulation by 1000 μL/L ethylene of average leaf lengths in tillers four through six of the first group of tillers in experiment four cannot be explained. It is possible that ethylene speeds the rate of leaf growth temporarily. From Figure 7 it is not possible to determine if the youngest leaves in tiller four of the first group were the same age or maturity across treatments. Perhaps the ethylene-treated leaves were growing at a faster rate and would be the same length as their counterparts at maturity. The oldest leaves of control and ethylene-treated plants were the same length.

No synergistic effect could be found in applying ethylene sequentially to ethephon. Some additive effects were shown in decreasing leaf length and shoot and plant weight and in increasing tiller internode elongation and stem/leaf weight ratios. Ethylene added to ethephon actually negated the restrictive effect ethephon had on

rhizome internode elongation. Ethephon did not, therefore, predispose Poa pratensis to ethylene sensitivity. This does not rule out, however, a contribution in growth regulation by some other component in ethephon catabolism. The growth regulation effects of ethephon and ethylene were similar but there were some notable differences. Ethephon treatment stimulated internode elongation as usual in experiment three while leaf elongation was not reduced. Ethylene at 100 μL/L had no effect in that experiment. Ethylene at 1000 μL/L in experiment four restricted leaf growth to the same extent as ethephon at 1600 mg/L with the exception of the leaf growth stimulation in tillers four through six in group one. Ethephon decreased rhizome internode number while ethylene did not. Ethephon caused greater tiller internode elongation than ethylene. Ethylene caused less leaf weight while ethephon did not. Ethephon caused greater leaf and axillary tiller numbers than ethylene.

Paired comparisons of ethephon and ethylene treatment at equal concentrations are needed in order to fully quantify the differences in their regulation of Poa pratensis growth. The conditions are now established for making those paired comparisons; an eight-day exposure period in a continuous air exchange system under greenhouse sun irradiance.

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GENERAL SUMMARY

Inconsistent efficacy has limited the application of turfgrass growth retardants to low-traffic, less-visible areas. More information is needed, not only regarding the interaction of growth retardants with the environment, but also in learning how plants regulate their own growth.

A three-year field study was conducted to determine if the seasonal growth phases of Poa pratensis had any effect on plant receptivity to five growth retardants. Mefluidide and amidochlor were more effective in spring, flurprimidol in summer, while ethephon and paclobutrazol were equally effective across seasons. The greatest differences in growth retardation appeared between the spring reproductive and summer vegetative growth phases. It is concluded, therefore, that the transition of Poa pratensis from its reproductive to vegetative phases affects its degree of response to turfgrass growth retardants. Ethephon was the only chemical to act as a true growth regulator by altering plant growth habit. Leaf elongation was restricted while internodes were stimulated to elongate from a normally compact stack of nodes.

Four laboratory experiments were conducted to determine conditions necessary for plant sensitivity to ethylene and to test the hypothesis that some component in ethephon degradation in addition to ethylene predisposes Poa pratensis to ethylene sensitivity. Ethephon was effective in most environments tested while ethylene was effective only after eight days of continuous application under full-sun conditions in

the greenhouse. Under those conditions, ethephon applied at 1600 mg/L and ethylene at 1000 μL/L had similar effects on tiller internode elongation, root weight and stem/leaf dry weight ratio. The effect of ethylene upon leaf length, however, varied from a decrease in some tillers, similar to that from ethephon, to an increase in other tillers, compared to the control. In that same experiment, ethylene treatment during ethephon degradation had an additive but not a synergistic effect on plant morphogenesis. Reduction in root growth was always associated with shortness in leaves. It is concluded that the reliability of ethephon effectiveness is due largely to its slow release of ethylene over a four to ten day period and that some threshold irradiance level is necessary for exogenouse ethylene at 1000 μL/L to cause a morphogenic response in Poa pratensis. Ethephon did not appear to predispose Poa pratensis to ethylene sensitivity, but the possibility of a contribution in growth regulation from some other component of ethephon degradation cannot be ruled out.

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